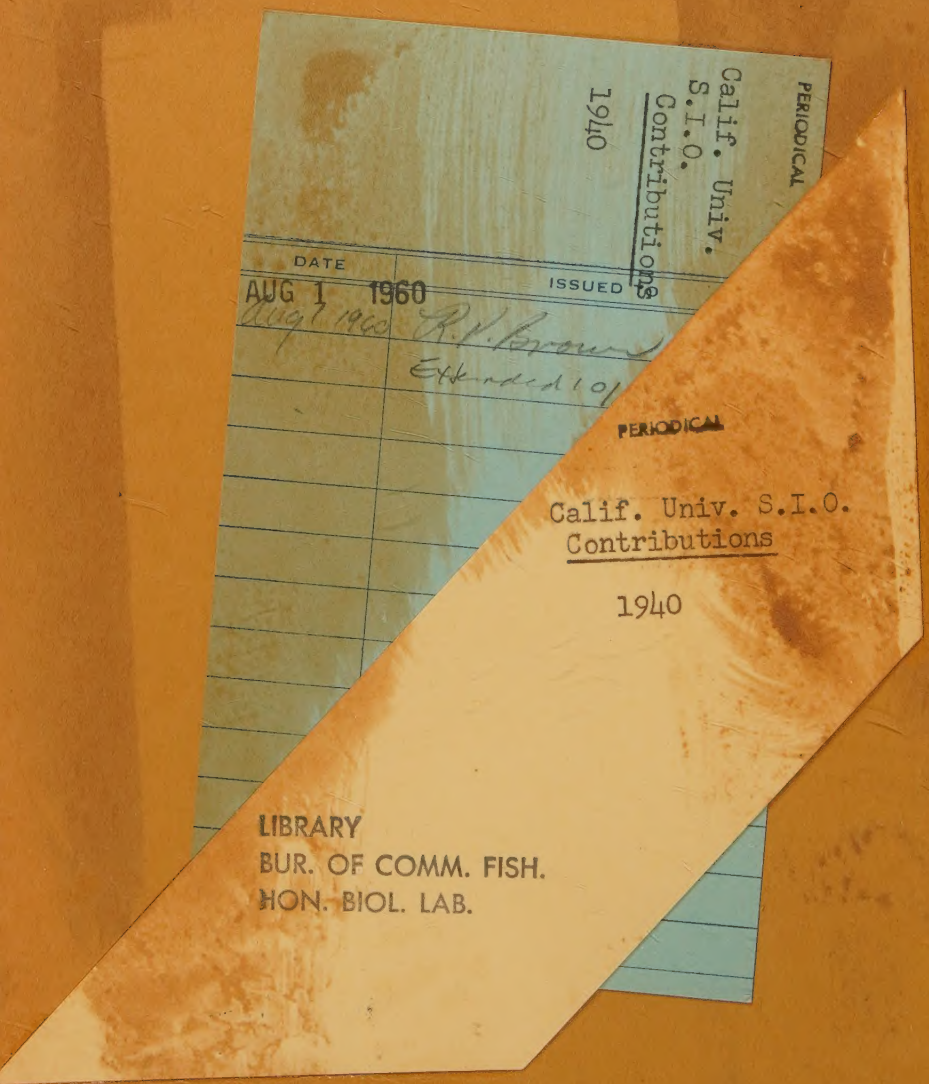
LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS


PERIODICAL
Calif. Univ.
S.I.O.
Contributions
1940
DATE
ISSUED
AUG 1 1960
Aug 1 1960 R.V. Brown
Extended 10/
PERIODICAL
Calif. Univ. S.I.O.
Contributions
1940
LIBRARY
BUR. OF COMM. FISH.
HON. BIOL. LAB.

SCRIPPS INSTITUTION OF OCEANOGRAPHY

UNIVERSITY OF CALIFORNIA

LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

CONTRIBUTIONS

1940

1714 Co

This volume contains contributions from the Scripps Institution of Oceanography which appeared during 1940 in publications other than *Bulletins of the Scripps Institution of Oceanography* and *Records of Observations of the Scripps Institution of Oceanography.*

LA JOLLA, CALIFORNIA

March, 1941

TABLE OF CONTENTS

Contribution No.

ALLEN, W. E.

Discolored sea water 99

Life in a drop of sea water 86

COE, W. R.

Notes on the morphology and sexuality of the terrestrial Nemertean *Geonemertes palaensis* 80

LA FOND, EUGENE C.

Sand movements near the beach in relation to tides and waves 107

LYMAN, JOHN, and RICHARD H. FLEMING

Composition of sea water 93

RITTENBERG, SYDNEY C.

Bacteriological analysis of some long cores of marine sediments 114

SCHEER, BRADLEY T.

Some features of the metabolism of the carotenoid pigments in the California sea mussel (*Mytilus californianus*) 112

SHEPARD, FRANCIS P.

Submarine geology and geophysics 111

SHEPARD, FRANCIS P., and EUGENE C. LA FOND

Sand movements along the Scripps Institution pier 83

SUMNER, FRANCIS B.

Further experiments on the relations between optic stimuli and the increase or decrease of pigment in fishes 82

The naturalist as a social phenomenon 97

Quantitative changes in pigmentation, resulting from visual stimuli in fishes and amphibia 98

SUMNER, F. B., and M. C. SARGENT

Some observations on the physiology of warm spring fishes 81

SVERDRUP, H. U.

The currents of the Pacific Ocean and their bearing on the climates of the coasts . . . 84

Hydrology, Section 2, Discussion. B.A.N.Z. Antarctic Research Expedition 1921-31, Reports. 91

On the annual and diurnal variation of the evaporation from the oceans 90

Research within physical oceanography and submarine geology at the Scripps Institution of Oceanography during April 1939 to April 1940 94

Trail blazing in the Pacific (Research in oceanography) 95

The unity of the sciences 113

Contribution No.

ZOBELL, CLAUDE E.

Effects of oxygen tension on the rate of oxidation of organic matter in sea water by bacteria 115

Some factors which influence oxygen consumption by bacteria in lake water - - - - - 96

ZOBELL, CLAUDE E., and JEAN E. CONN

Studies on the thermal sensitivity of marine bacteria - - - - - - - - - - - - - - 92

ZOBELL, CLAUDE E., and JANICE STADLER

The effect of oxygen tension on the oxygen uptake of lake bacteria - - - - - - - - 88

LIST OF CONTRIBUTIONS, new series.

Contribution No. 80

OCCASIONAL PAPERS
OF
BERNICE P. BISHOP MUSEUM
HONOLULU, HAWAII

Volume XV January 10, 1940 Number 19

Notes on the Morphology and Sexuality of the Terrestrial Nemertean, Geonemertes palaensis[1]

By W. R. COE

OSBORN ZOOLOGICAL LABORATORY, YALE UNIVERSITY, AND SCRIPPS INSTITUTION OF OCEANOGRAPHY[2], UNIVERSITY OF CALIFORNIA

A collection of 24 specimens of *Geonemertes palaensis* Semper which the writer has had the opportunity of studying through the courtesy of Bernice P. Bishop Museum includes a series of sexual phases which are thought to be typical of the normal sexuality of the species. Consequently the collection is of much interest. A complete account of these phases has not been possible hitherto because of lack of suitable material. A few details of other anatomical features supplementary to those previously reported can also be supplied at this time.

This collection was made by Y. Kondo, a member of the Micronesian Expedition in March, April, and May 1936, and of the Henry G. Lapham Expedition in July 1938, at the following localities:

Palau Islands: Anguar (near hospital), Koror and Komakam (northeast corner of island), Peleliu; Caroline Islands: Yap (Mount Matade, Okau district), Ponape, Jokaj Islet, Nanpilo [Nanepil]; Samoan Islands: Pago Pago.

This species has been collected previously from the Palau, Celebes, Kei, and Samoan Islands at various situations from sea level to nearly 700 meters elevation. It is reported as common in Samoan forests. A closely similar species (*G. arboricola*) has been found on the Seychelles Islands in the Indian Ocean. The ten other terrestrial species at present known are endemic in Rodriguez Island, Bermuda, New

[1] Micronesian Expedition Publication 4.

[2] Contributions from Scripps Institution of Oceanography New Series, no. 80.

Zealand, Australia, New Guinea and Auckland Islands. Two of these species have been introduced into greenhouses in Germany.

In addition to the investigations of Von Kennel (1878), Dendy (1893), Böhmig (1898), Coe (1904), Schröder (1918), and others on the morphology and biology of various species of terrestrial nemerteans, Hett (1928) and Stammer (1934) give brief synopses of the characteristics and known distribution of each of the 12 described species.

Waterston and Quick (1937) have recently found an Australian species (*Geonemertes dendyi*) living beneath stones and fallen branches in damp situations at several localities near Swansea, Wales, where it has evidently become acclimated. The worms were observed to feed by sucking the juices of minute bugs and *Collembola*. Only females have been found, but some of these deposited clusters of eggs which developed by the direct method and liberated the young worms in about three weeks.

Geonemertes palaensis was described by Semper in 1863 from individuals found on the Palau Islands. The specimens in the present collection are all rather small, measuring only 10 to 28 mm. in length after preservation, the largest being less than half as long as some of the others that have been previously collected. The smallest ones represent young individuals, and these are of special interest in that they show the early sexual conditions necessary for the elucidation of the sexual phases of the entire life history. Most of the specimens previously studied have been considered females.

These specimens allow the following supplementary details to be added to the morphological characteristics previously recorded for the species by Von Kennel (1878), Böhmig (1898), Schröder (1918), Hett (1928), and earlier investigators.

Ocelli: They have one pair of large dorsal ocelli and from 1 to 3 pairs of small ocelli.

Proboscis: Most of these specimens have only two pouches of accessory stylets, but several of them have four. They have from 16 to 21 proboscidial nerves.

Nerve cords: The lateral nerve cords have well differentiated dorsal cores of fibers arising from the dorsal ganglia.

Nephridia: The nephridial system as described by Schröder (1918) and supplemented by Coe (1929) consists of thousands of

independent protonephridia, the system extending in the parenchyma from the tip of head to the posterior end of body. In the brain region and immediately anterior thereto the flame cells are massed about the cephalic blood vessels into veritable nephridial "glands" with several hundred flame cells in a single transverse section of the head (fig. 1). The preservation was not sufficiently perfect to allow the delicate efferent ducts as described for *G. agricola* (Coe, 1929) to be distinguished. The crowding of the flame cells is naturally greatest when the blood vessels are empty.

Sexuality of other species: According to the published descriptions there is great variation in the sexual conditions of the 12 known species of terrestrial nemerteans. Three species (*G. australiensis* Dendy, *G. rodericana* (Gull.), and *G. hillii* Hett) are described as of separate sexes, with the males smaller than the females. Three others (*G. dendyi* Dakin, *G. graffi* Bürger, and *G. novae-zelandiae* Dendy)

FIGURE 1.—Section of cephalic blood vessel with surrounding nephridial gland; *bv*, distended portion of vessel; *bv'*, contracted portion of vessel, showing darkly stained endothelial cells which act as valves when vessel is contracted; n^1, flame cells, surface view, showing the two terminal nuclei; n^2, same in section; n^3, same, showing but one of the two terminal nuclei; n^4, transverse sections of flame cells; n^5, single flame cell more highly enlarged.

have been thought to be of separate sexes, although no males have been found. One species (*G. spirospermia* Darbishire) is known only from a single male and another (*G. caeca* Darbishire) from a single female. Because of the scanty material which has been available for the study of these 8 species the evidence that hermaphroditism, either functional or sequential, does not occur in at least some of them is far from satisfactory. The remaining 4 species (*G. agricola* Will.-Suhm, *G. arboricola* Punnett, *G. chalicophora* Graff, and *G. palaensis* Semper) are undoubtedly hermaphroditic.

Reproductive organs: The sexual conditions in *G. palaensis* have hitherto been in some doubt, since all but one of the specimens studied have been considered to be females. The species now proves to be irregularly protandric, as suspected by Schröder (1918) and hermaphroditic, as reported by Von Kennel (1878), with alternating male and female functional sexual phases. The female phases, however, are usually complicated by the precocious development of a few or many ripe spermaries of the normally following male phase before the ova are fully mature (figs. 2, 3). Likewise in the primary male

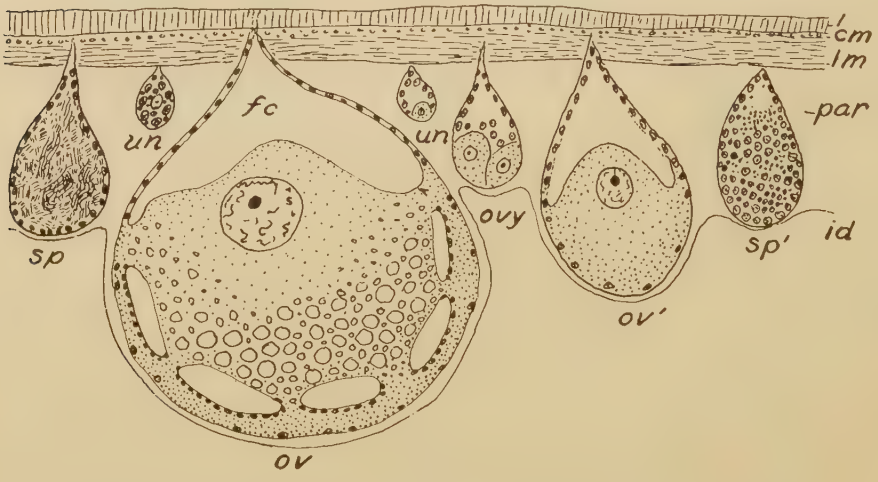


FIGURE 2.—Portion of horizontal section of body, dorsal to nerve cord, of functionally hermaphroditic individual; *ov*, ripe ovary with its single ovum, oviduct and fertilization chamber (*fc*); *ov'*, immature ovary; *ovy*, young ovary with two ovocytes; *sp*, ripe spermary; *sp'*, immature spermary; *un*, two sexually undifferentiated gonads; *i*, epithelium of body wall; *id*, intestinal diverticula; *cm* and *lm*, circular and longitudinal musculatures of body wall, respectively; *par*, parenchyma. (Slightly diagrammatic.)

phase of the young individual at first sexual maturity the ovaries often begin development before the sperm are discharged (Coe, 1939). The terminal portion of the female phase is therefore usually functionally hermaphroditic and self-fertilization in isolated individuals may be assumed as highly probable.

The primary functional male phase of the young worm is thus followed by successive, more or less regularly alternating, female and male phases, although the female phase, as stated above, is usually functionally hermaphroditic at the time of ovulation. Since each gonad functions but once and new gonads are constantly forming as the older ones are being emptied, the proportion of male and female gonads at different times in the same individual is highly variable. Moreover the evidence from a related species (*G. agricola*), of which a large number of living individuals have been studied, indicates that there are individual, perhaps hereditary, differences in respect to the relative dominance of male and female characteristics (Coe, 1904).

The sexual life history of a typical individual may be summarized as follows: primary male phase, with cross fertilization, followed by female hermaphroditic phase, with provisions for self-fertilization in isolated individuals. After a period of recuperation a secondary male phase begins a new sexual cycle, also with intergrading sexual phases, and this may be repeated.

The sexual condition of preserved specimens can only be determined with accuracy by examining sections throughout the entire gonadal region, for it often happens that localized groups of gonads are in a different sexual condition than those in other parts of the body. Consequently the conclusion that all except one of the specimens of this species previously examined were females may be accepted with some hesitation. It is highly probable that the three functional females in the present collection represented a temporary female phase only. No collector, so far as is known, has yet secured sufficiently young individuals to show the very first stages of sexual maturity. The two functional males in this collection were already provided with immature ovaries.

Of the 24 specimens in this collection, 2 were functional males at the time of collection, with ripe spermaries and immature ovaries, as mentioned; 3 were functionally female, with ovaries showing various early stages of ovogenesis but no spermaries; 9 were unripe sexually,

with small ovaries and undeveloped spermaries, and 10 were functional hermaphrodites with large ova and ripe or nearly ripe spermaries. The 9 sexually unripe individuals were not young but evidently represented a stage immediately following a period of sexual activity during which both ovaries and spermaries were completely emptied.

The new gonads which are constantly forming during the entire lifetime, following first sexual maturity, originate from a band of primordial sexual cells which extends throughout the gonadal region of the dorsal side of each of the nerve cords. In exceptional individuals, one or more spermaries, but not ovaries, may be formed on the ventral side of the nerve cord or even ventral to the lateral blood vessel. The young gonads are at first sexually undifferentiated and essentially ambisexual in nature. Antecedents of both types of sexual cells are present (figs. 2, 3). As the one type becomes activated, the other type gradually disappears by cytolysis.

The conditions which determine whether the young gonad is to form an ovary or a spermary are not known. In general, a spermary develops when numerous large ovaries are nearby, the spermary then forming from an undifferentiated gonad between the ovary and the nerve cord. Hence it may be suggested that unfavorable nutritive conditions may contribute to the differentiation of a spermary, since the

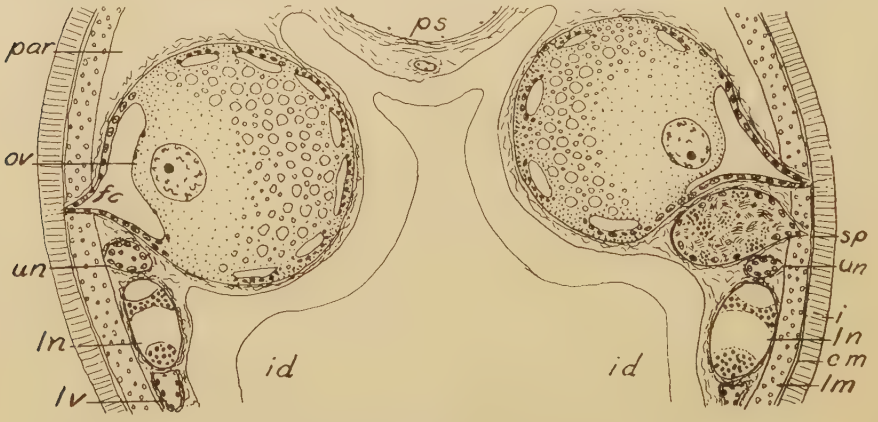


FIGURE 3.—Portion of transverse section of body of functionally hermaphroditic individual; *ov,* ripe ovaries with oviducts and fertilization chambers (*fc*); *sp,* ripe spermary; *un,* two undifferentiated gonads; *ln,* lateral nerve cord with dorsal and ventral fibrous cores; *lv,* lateral blood vessel; *ps,* proboscis sheath; *i,* epithelium of body wall; *id,* intestinal diverticula; *cm* and *lm,* circular and longitudinal musculatures of body wall, respectively; *par,* parenchyma.

rapidly growing large ova may exhaust the available nutritive material in the vicinity. In support of this hypothesis it may be mentioned that gonads in abnormal positions are always spermaries. It is also conceivable that the growing ova or their associated cells may secrete a substance of a hormonal nature to which the primary spermatogonia are chemically sensitized and thereby activated.

Ovaries are usually much more numerous than spermaries, the ratio being in some individuals upwards of a hundred to one. This may be another reason why nearly all the specimens previously collected have been classed as females. Also the spermaries come to maturity much more rapidly than do the ovaries.

Fertilization in all the terrestrial species, insofar as is known, is internal and the intimate association of two or more sexually mature individuals has been observed in other species (Dendy, 1893; Coe, 1904).

G. palaensis is presumably usually, if not invariably, oviparous, since no evidence of viviparity has been observed and an egg cluster was found attached to a specimen studied by Hett (1928). Only one species (*G. agricola*) is definitely known to be viviparous (Coe, 1904).

LITERATURE CITED

Böhmig, L., Beiträge zur Anatomie und Histologie der Nemertinen, Zeitsch. f. wiss. Zool., **64**:479-564, 1898.

Coe, W. R., The anatomy and development of the terrestrial nemertean (Geonemertes agricola) of Bermuda, Boston Soc. Nat. Hist., Proc., **31**:531-570, 1904.

Coe, W. R., The excretory organs of terrestrial nemerteans, Biol. Bull., **56**:306-311, 1929.

Coe, W. R., Sexual phases in terrestrial nemerteans, Biol. Bull., **76**: 416-427, 1939.

Dendy, A., Notes on the mode of reproduction of Geonemertes australiensis, Roy. Soc. Vict., Proc., **5**:127-130, 1893.

Hett, M. L., On some land nemerteans from Upolu Island (Samoa) with notes on the genus Geonemertes, Zool. Soc., London, Proc., (1927), pp. 987-997, 1928.

Kennel, J. von, Beiträge zur Kenntniss der Nemertinen, Arb. Zool.-zoot. Inst. Würzburg, **4**:305-381, 1878.

Schröder, O., Beiträge zur Kenntniss von Geonemertes palaensis Semper, Senkenburg, natur. Gesellschaft, **35**:155-177, 1918.

Stammer, H. J., Eine für Deutschland Neue eingeschleppte Landnemertine, Geonemertes dendyi Dakin, mit einer Bestimmungstabelle der Gattung Geonemertes, Zool. Anz., **106**:305-311, 1934.

Waterston, A. R. and Quick, H. E., Geonemertes dendyi Dakin, a land nemertean, in Wales, Roy. Soc. Edinburgh, Proc., **57**:379-384, 1937.

Contribution No. 81

Reprinted from Ecology, Vol. 21, No. 1, January, 1940
Printed in U. S. A.

SOME OBSERVATIONS ON THE PHYSIOLOGY OF WARM SPRING FISHES[1]

F. B. Sumner and M. C. Sargent
The Scripps Institution of Oceanography, La Jolla, California

Numerous experiments upon cold-blooded animals have shown that their respiratory metabolism is a function of the temperature to which they are subjected. In the case of fishes, several criteria of respiratory metabolism have been employed: (1) actual oxygen consumption, as revealed by direct measurement; (2) oxygen requirement, as indicated by (*a*) survival time in deoxygenated water, or (*b*) survival time in dilute potassium cyanide solution. In this laboratory, all three of these procedures have been employed, with results which appear to be in substantial agreement (Sumner and Doudoroff, '38). At different temperatures, the reciprocals of the times of survival of fishes in thousandth-molar KCN solution are in very nearly the same ratio as the measured rates of oxygen consumption at the same temperatures, while the ratio for survival time in boiled sea-water may be regarded as reasonably close.

The mean Q_{10} for respiratory metabolism in *Fundulus parvipinnis,* based upon direct measurements of oxygen consumption by Wells (1935, table II, experiments 4 and 5, means of three figures: 10° to 20°, 12° to 22°, and 14° to 24°) was 2.90. The mean Q_{10} for the goby, *Gillichthys mirabilis,* within approximately the same temperature range, based upon reciprocals of survival time in KCN solution, was 2.84 (Sumner and Doudoroff, '38, table I). The corresponding figure, based upon a much smaller series, tested in boiled sea-water, was considerably lower, it is true, *viz.,* 2.49.

Further experiments have shown that the initial change in susceptibility to cyanide, resulting from an increase or decrease in temperature, was followed by a "recoil," such that the departure of each lot from its original metabolic level diminished somewhat with the lapse of time. Graphs (Sumner and Doudoroff, '38, fig. 2) show that the greatest difference between two lots kept at contrasting temperatures is manifested shortly after their first being subjected to these temperatures. Thereafter the difference diminishes for a few days. This process of physiological adaptation appears to be brief, however. After ten days or less, there is no further visible convergence of the curves for the two lots, kept at 10° and 30°, respectively. These continue to manifest the greater part of the original difference, their mean periods of resistance to KCN, at the end of a month, standing in the ratio of about 6 to 1.

So far as we know, previous tests of the relation of temperature to the respiratory metabolism of fishes have concerned themselves with changes under laboratory conditions, the duration of the treatment being at most a few months. That fishes living under natural conditions in warm and cold waters should maintain throughout their lives such extreme differences in oxygen consumption would seem on first thought unlikely. This if only because we know that some of the most active fishes (*e.g.* the trouts of mountain streams) spend their lives in cold waters.

It has long seemed desirable that comparative tests of metabolism should be made upon fishes in nature, preferably in some case in which isolated populations of the same or closely related species are found in waters of widely different temperature. It is well known that members of the genus *Cyprinodon* occur in numer-

[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 81. Services were rendered by various persons throughout these studies under W.P.A. Project 665-03-3-141.

ous desert springs in California and neighboring parts of Nevada. Much less generally known is the existence of another genus of poeciliid fishes (*Crenichthys* Hubbs) which appears to be rather widely distributed in the springs of eastern Nevada. Many of these springs are warm or temperate ones, which are believed to maintain fairly constant temperatures throughout the year. In some cases, at least, these fishes appear to restrict themselves very largely to the actual sources of flow, not venturing far into the brooks or creeks which proceed from them. So far as this is true, their thermal environment must present little variation throughout their lives. This group might be expected to furnish, therefore, particularly favorable material for experimental studies of the type above suggested.

In April and May, 1939, the authors spent two weeks in the field, in quest of *Cyprinodon* and in experiments upon one species of this genus. Later in the year (October), another two weeks were devoted to field studies of *Crenichthys*. Our advance information regarding the occurrence of both of these fishes was received almost wholly from Mr. R. R. Miller, of the University of California (now of the University of Michigan), who provided us with abundant records of field data, obtained by Professor C. L. Hubbs and himself. Our thanks are due Mr. Miller for indispensable help in this connection.

Members of *Cyprinodon* inhabiting these various desert springs have been generally referred to a single species, *C. macularius* Baird and Girard. Pronounced local differences in size and color are evident among these fishes, however, and recent students believe that some of these forms deserve specific rank. Likewise, but a single species of *Crenichthys* (*C. nevadae* Hubbs) has thus far been described (Hubbs, '32), though it is possible that the occurrence of these fishes in isolated springs has led to their subspecific or even specific differentiation.[2] However, these taxonomic questions hardly seem relevant to our present discussion and we have attempted no taxonomic study of the specimens collected by us. We understand that such studies are being conducted by others.

Both of the species here under consideration are small fishes, rarely reaching a length of 6 centimeters. *Crenichthys* differs from *Cyprinodon* in altogether lacking the pelvic fins and in dental and some other characters. There are considerable sexual differences in color and markings, and, particularly in *Crenichthys*, there is wide individual variability in these respects.

Fish Slough, California.—As our intended "cold" station, we first visited Fish Slough, some ten miles north of Bishop, California, where *Cyprinodon* was known to occur, and where the water was believed to remain low (20° C. or below) throughout the year. Fish Slough (U. S. G. S., "Bishop" Quadrangle) is essentially a creek, bordered by narrow strips of marshy land, and heading in a considerable number of large springs.

It had been planned to transport fishes from these springs to the warm-spring region next to be visited in Nevada. Although this proved to be impossible, a brief statement regarding these fishes and their habitat seems worthwhile.

While never concentrated in schools of any size, they were present in some numbers in or near the springs. Nearly a hundred were caught by our party with seine and dip-net, within the course of a few days, and without greatly depleting the visible stock. Of the specimens captured, the sex of only 60 was recorded. Twenty-five of these were males, 35 females. The water temperature, on April 23–27, in and near the springs, ranged

[2] Since writing the foregoing, we have learned from Dr. Hubbs (personal communication) that he now recognizes a second species of *Crenichthys* (*C. baileyi* Hubbs), and that the specimens obtained by us are to be referred to this species.

from 19.2° to 20.8° C.[3] The fishes appeared to be in full sexual activity. Spawning movements were continually observed, though it was impossible to approach closely enough to witness the actual discharge of eggs.

We were surprised by the low viability of these fishes in captivity, since "desert minnows" of this genus have frequently been transported successfully to aquaria in San Francisco and elsewhere (Cf. also experiments with *Crenichthys,* below). Our specimens frequently died within a few hours after capture, although handled with great care, and the majority of them died within a day or two, even when kept in screen cages immersed in the springs from which they had been caught. Very few reached our Nevada camp alive, and these were presumably in no condition for physiological tests. There was no appearance at any time of asphyxiation. This unexpected mortality may possibly have been due to exhaustion from prolonged sexual activity, which seemed to continue unabated in the cans or cages in which the fishes were forced into rather close association.

Ash Meadows, Nevada.—For the foregoing reason, our tests of metabolism on this trip were restricted to the "Ash Meadows" district of the Amargosa Desert, in southwestern Nevada, about 12 miles from Death Valley Junction, California. This region abounds in springs of considerable size, having temperatures ranging from 23° to 33.5° C. Most of these springs, together with their outflowing streams in the immediate neighborhood, are inhabited by *Cyprinodon,* sometimes in great abundance. Some of them contain other small fishes (Cyprinidae).

The highest temperature noted (33.5°) was in Devil's Hole, a shallow cave containing a small pool, the outlet from which does not flow above ground. Here occurs a minute, dark colored *Cyprinodon,* which has been provisionally described by Wales ('30) as a distinct species (*C. diabolis*). The entire existing population of this form can hardly exceed a few hundred individuals.

Our experiments were restricted to the two springs in this locality which displayed (nearly) the greatest contrast in temperature, and from which *Cyprinodon* could be obtained. The warm spring was on the ranch of Ora Lovell, the cool one on the ranch of R. M. Tubb. We are indebted to Mr. Lovell and to Mr. Tubb and his family for the opportunity to catch our specimens and for other favors.[4]

These experiments, though decisive on some points, were rather rigidly restricted by the time at our disposal and by the extent of one of the two essential populations. It was even necessary to omit at this time the obviously important experiment of testing the cool spring fishes at the temperature of the warm spring.

The Lovell spring, at the time of our visit (April 28 to May 1) had a temperature of 32.5° to 33° C. This temperature did not fall appreciably between the points of outflow and the nearby pool, where the fishes congregated in large numbers, and from which most of our specimens were caught with a small seine.

The temperature of the Tubb spring maintained itself (April 28 to May 4) at 23.8° to 24°.[5] The supply of *Cyprinodon* was much more limited here. Most of our specimens were caught, one at a time, with a dip-net.

The successful experiments involved the determination of the survival time of these fishes in 0.001 M KCN. Death, in these experiments, was counted from the

[3] Mr. Miller reports a temperature of 64° F. (17.8° C.) for August 2, 1937. This is rather surprising, considering that our readings were made in April.

[4] Our acknowledgments should include mention of the manifold services of Mrs. Grace Sargent and Mrs. Margaret Sumner, who accompanied us on this and the later field trip. Mrs. Sargent is responsible for the capture of many of the specimens and for some of the cyanide tests.

[5] The temperatures recorded by us for both of these springs agree almost precisely with those found by Dr. Hubbs and Mr. Miller during a previous summer.

moment that an individual ceased to make any visible movements, either spontaneous, or provoked by poking with a glass rod. The conspicuous death-throes, described for *Gillichthys* (Sumner and Doudoroff, '38), were rarely shown by *Cyprinodon*. Our experiments were of three sorts:

(1) Fifty-two specimens (33♂, 19♀) from Lovell's spring (warm) were tested at approximately their habitual temperature. They were placed, about 30 minutes after capture, in KCN solution, in three bowls, immersed in the water from the spring. The temperature in the bowls commenced with 32.5°, falling to 31.5° toward the end.

(2) Thirty-three fishes (21♂, 10♀, 2?) caught in Tubb's spring (cool), were tested at the approximate temperature of the latter. The temperature in the bowls was 23.8° ±, falling 1° or less during the tests. Three tests were made on different days.

(3) Forty fishes from Lovell's spring (20♂, 20♀) were brought almost immediately to Tubb's, their water temperature being allowed to fall to that of the latter. About one hour after capture they were placed in KCN in three bowls, immersed in the stream from the spring. The temperature in the bowl was 23.7°, falling only 0.2° at the end.

The mean survival times of these three series are given in table I.

TABLE I. *Mean survival times of fish in KCN solution*

	Number of fishes	Time in minutes
Lovell's at Lovell's	52	41.6
Tubb's at Tubb's	33	65.0 [6]
Lovell's at Tubb's	40	96.0

The possibility that the differences among these three series resulted from any chance differences in the proportions of males and females seems to be excluded. The array of values in the largest series (series 1, fig. 1), reveals no tendency toward a bimodal distribution. It must likewise be pointed out that the sex-ratios of series 1 and 2 were not widely different from one another, although series 3, it is true, differs greatly from the other two in this respect. The excess of males recorded for the Ash Meadows fishes as a whole contrasts with the situation at Fish Slough, where females rather heavily preponderated among the specimens saved. That the former circumstance was not altogether due to a tendency on our part to select larger individuals for experiment (the males are larger than the females), is shown by the composition of the Tubb's spring lot, which includes nearly all the individuals taken. Since a preponderance of males is quite unusual in a fish population, it is possible that the males frequented more accessible parts of this very deep spring.

It was not regarded as necessary to measure these fishes, as had been done in the goby experiments, since it was determined for the latter that size, within very broad limits, played no part in susceptibility to cyanide. Casual observation pointed to a similar lack of correlation in the case of *Cyprinodon*.

Histograms (fig. 1) show the mortality rates of these three sets of fishes. The probability that the difference between the mean value of series 1 and that of either series 2 or 3 is accidental is much less than 1 in 10,000. In the case of the difference between series 2 and 3, the probability is considerably greater, though still small, viz.: about 35 in 10,000.

Of course, statistical probabilities such as these serve merely to exclude "chance" (*i.e.*, random sampling) as an explanation of the differences in question. The actual cause of the differences may be quite irrelevant to the objects of the experiment. In this connection, it is important to state that our later series of experiments with another species of fish

[6] The times recorded for the three separate tests here averaged were: (1) 91.3 (6 fishes); (2) 53.8 (16 fishes); (3) 66.8 (11 fishes). The high first figure is largely due to the prolonged survival of a single individual (see figure 1 (2)).

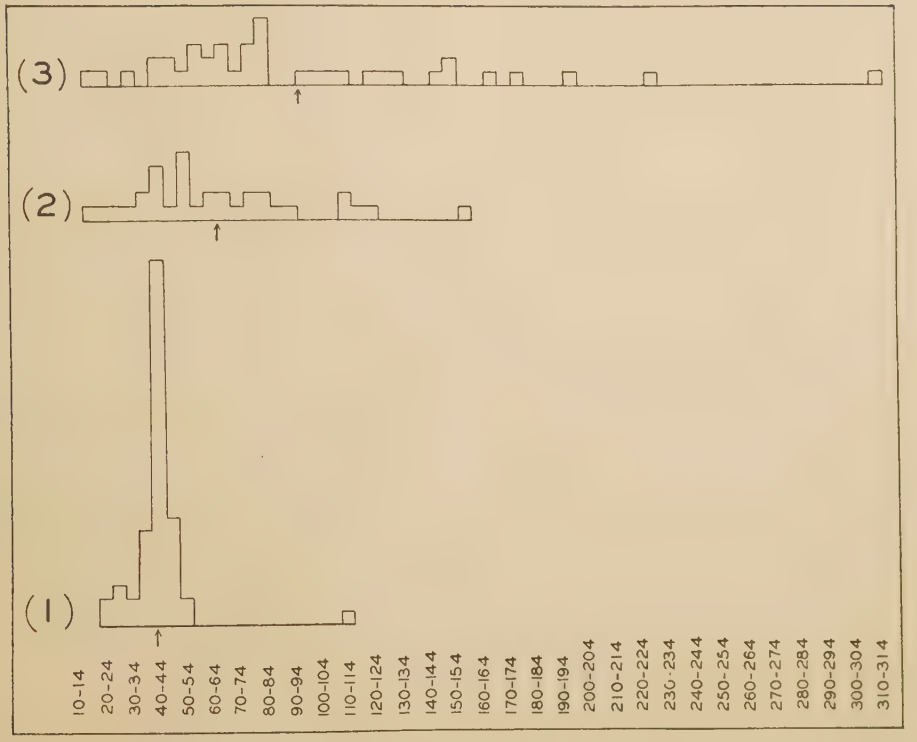


FIG. 1. Time of survival of *Cyprinodon* in thousandth-molar potassium cyanide. (1) Warm-spring fishes, tested at their normal temperature (32.5°). (2) Cool-spring fishes, tested at their normal temperature (23.8°). (3) Warm-spring fishes, tested at temperature of cool-spring. Abscissas denote times in minutes. Each square represents an individual fish. Arrows indicate means.

(p. 52) failed to indicate any such superior resistance on the part of warm-spring individuals, when transferred to a cool spring, in comparison with those native to the latter. This difference between our two sets of results may, however, depend upon differences in the species employed, or upon differences in their environmental conditions, so that we seem warranted in admitting the possibility that the picture presented by our table I and figure 1 represents the typical reactions of *Cyprinodon* (sp?) under the three stated sets of conditions.

It will be noted that the mean survival time of the warm-spring fishes at the cold-spring temperature (96 minutes) was 2.31 times that of these same fishes at their own habitual temperature (41.6 minutes). Since the difference in temperature between these two springs was close to 9° C. the Q_{10} for respiratory metabolism, as thus revealed, was 2.5 ($=2.31^{10/9}$).

No very exact comparison with Q_{10} figures for the goby *Gillichthys* (Sumner and Doudoroff, '38) is possible, owing to differences in the conditions of the two sets of experiments. Not only were the temperature ranges different in the two cases, but most of the figures for *Gillichthys* are based upon experiments in which the tests were made from one to many days after the transfer of the fishes to warmer or cooler water. Such tests were impossible in the case of *Cyprinodon*, owing to the difficulty of maintaining this fish in health for so long a period.

For gobies, the Q_{10} figure, between 20° and 30°, based on fishes which had been

kept for some weeks at the latter temperature, was 2.1; while the figure based on fishes kept for a very brief period (from a half hour to five hours) at this temperature was 2.0 (Sumner and Doudoroff, '38, table II). The latter figure is probably more fairly to be compared with the figure above stated for *Cyprinodon,* although the temperature change was in the opposite direction.

If, on the other hand, we compare the metabolic rate of the Tubb spring (cool water) fishes at their accustomed temperature (series 2) with that of the Lovell spring fishes at their accustomed temperature (series 1), we find an increase, per 9° of 1.56, indicating a Q_{10} of 1.6. One might be tempted to hold that the difference between this figure and the one which is based upon a comparison of series 1 and 3 (2.5) furnished a rough measure of the degree of divergent temperature acclimatization which our two populations had undergone. However, the failure of *Crenichthys* to manifest similar relations weakens the case for this interpretation of the phenomena.

In view of the foregoing considerations, it was regarded as important, after our visit to eastern Nevada in the fall, to repeat, in part, our Ash Meadows experiments. A serious attempt was made to do this, but changes which had been made in the outflow of the water at the Tubb spring rendered this impossible.

White River Valley, Nevada.—Despite its name this valley contains no continuous, permanent river, at least at the levels visited by us. It contains, however, numerous large springs having various temperatures. Our headquarters for about two weeks in October, 1939, were made near Preston, White Pine County, close to a large spring, or group of springs, having relatively low temperatures. "Preston Spring," as we shall designate this, is the source of a creek of considerable size, which is used locally for irrigation purposes. Its temperature, at several of the points of outflow, was 21.0° C., throughout the period of our visit (October 4 to 16).[7]

Small fishes of several species are abundant in the upper reaches of this creek. Besides *Crenichthys baileyi* Hubbs, a catostomid (*Pantosteus* sp.) and a cyprinid (*Rhinichthys osculus*) were taken. These were all kindly identified for us by Dr. Hubbs. The first named, which was our main object of interest, could be caught in dip-nets in sufficient numbers for experimental purpose. Another favorable circumstance was the ability of these fishes, both those from the cool and the warm spring, to withstand captivity and transportation with little or no resulting mortality.

The warm spring with which we were concerned is known locally as "Mormon Spring." It is located in Nye County, about thirty miles to the south of Preston and about 6 miles west of Riordan's

[7] This is slightly lower than the figure (71° F.) given by Dr. Hubbs for August 26, 1938.

TABLE II. *Oxygen determinations from two Nevada springs*

Preston Spring (cool)			Mormon Spring (warm)		
Locality	Number of samples	ml O_2/l	Locality	Number of samples	ml O_2/l.
Source 1	4	2.04	Source	2	0.38
Source 2	2	2.25	West ditch, below small spillway	2	2.09
Source 3	2	2.14	Same, farther down	2	2.56
Creek, ¼ mile below sources, sunrise	1	2.94	East ditch	2	2.12
Same, 3 P.M.	2	4.35			

ranch. The temperature of this spring, at its main point of outflow, is almost exactly 37.0° C. *Crenichthys* was abundant here, but no other fishes were seen. While they swam freely into the warmest water, most of our specimens were obtained some yards further down-stream, where the temperature fell to 36° or even lower.

Oxygen determinations by the Winkler method (table II) showed that the waters from these two springs differed widely in respect to oxygen content at their sources. That discharged by the warm spring contained about a sixth as much oxygen as that from the cool one. It will be seen, however, that the former water soon acquires an oxygen content closely similar to that of the latter, after exposure to aeration and to the photosynthesis of algae. The effects of these influences upon the water of Preston Spring are likewise shown.

Tests of metabolic rate, by the cyanide method, were made in four series of experiments (table III). In each of these experiments, it was our practice to immerse the bowls containing the KCN solution in the water of the spring where the test was made, with the object of keeping them at the temperature of the latter. In reality, however, the temperature in the bowls commonly fell from 1.5° to 3° C. in the course of the experiments. In experiments involving transfer from one spring to the other, the fishes were carried in somewhat insulated 3-gallon bottles. This involved a delay of several hours, during which the water temperature fell about five degrees.

TABLE III. *Mean survival times of warm-spring and cool-spring fish in KCN solution in water of their own and another spring*

	Number of experiments	Number of fishes	Mean survival times	Coefficient of variation
(1) Mormon at Mormon	3	48	9.67	14.9
(2) Preston at Preston	3	83	44.7	15.9
(3) Mormon at Preston	3	98	41.9	18.0
(4) Preston at Mormon	5	52	5.81	16.5

Table III gives the mean survival times and other data for these various tests, while figure 2 presents the distribution of frequencies.[8]

(1) The mean survival time of the first series (warm-spring fishes tested at their customary temperature) is about 0.22 that of the second series (cool-spring fishes tested at their customary temperature), if the figure for the latter which appears in the table be employed. It is 0.24, if a rejected experiment (see next paragraph) be included. Another comparison of interest is that between the survival time of the warm-spring fishes when tested in the latter, and that of the cold-spring fishes when transferred to the warm spring. It will be seen that the former is 66 per cent greater than the latter. This point will be discussed below.

(2) The "Preston at Preston" series, as included in table III, comprises three experiments, the mean survival times for these being 40.5, 43.5 and 51.9 minutes, respectively. In each case, the fishes were kept over night in screen cages, immersed in the spring, before the test was made. A fourth experiment, based upon 44 individuals, has been rejected from this series, owing to the somewhat enfeebled condition of the fishes.[9] The mean survival time of this lot was 29.7 minutes. To include these would lower the grand average to 39.5.

The figures for these first two series —9.67 and 44.7 (or 39.5) minutes—afford a comparison of the resistance to KCN of two lots of fishes dwelling in environments differing by about 15° C. in temperature. They indicate a Q_{10} of 2.8, or 2.6, if the more inclusive of the foregoing means is accepted for the Preston fishes. These figures approximate certain of those for the Q_{10} as determined

[8] Identification of the sexes was impossible in so many cases that we have thought it best not to give any figures for these. Apparently the females were greatly in excess.

[9] This lot was exceptional in having been subject to a considerable mortality during the preceding 24 hours.

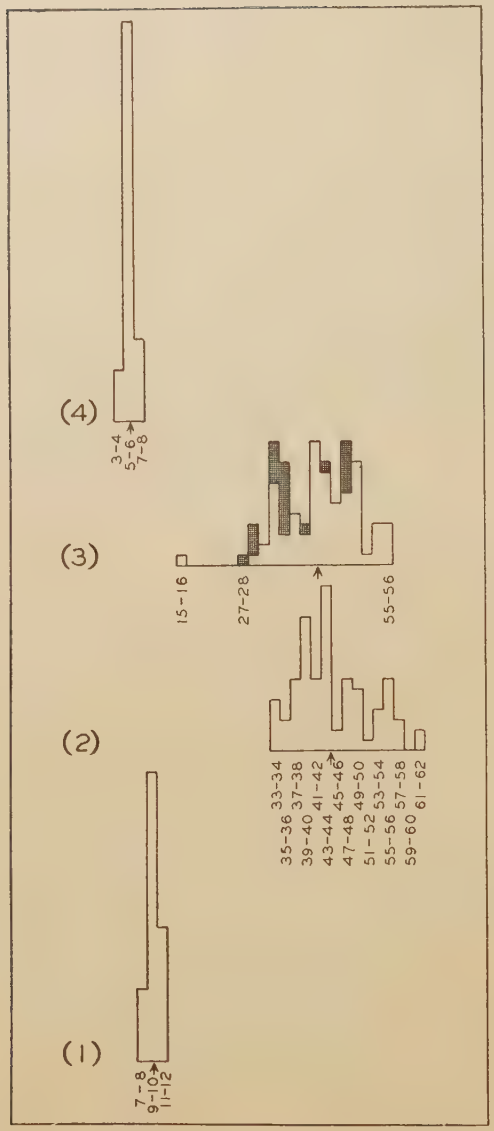


FIG. 2. Time of survival of *Crenichthys:* (1) Warm-spring fishes tested at (nearly) their normal temperature (35.5°–36°). (2) Cool-spring fishes, tested at (nearly) their normal temperature (21°). (3) Warm-spring fishes tested at temperature of cool spring. Shaded areas represent fishes kept over night in latter. (4) Cool-spring fishes tested at temperature of warm spring (see fig. 1).

from laboratory studies of the goby *Gillichthys,* though not very closely that figure which is most nearly comparable with them. They likewise approximate the Q_{10} figure observed in transferring Lovell's spring fishes to Tubb's spring, though not that based upon Lovell's and Tubb's spring fishes at their own natural temperatures, which is considerably lower (Cf. p. 50).

(3) The "Mormon at Preston" figures are likewise based upon several experiments. In this case, the conditions were purposely made somewhat different in the different experiments. In one case (*a*), the test was made without any preliminary sojourn in Preston Spring water. In the second case (*b*) the fishes were kept in a screen cage, in the Preston Spring for 2½ hours before the test. In the third case (*c*), they were kept in the latter for 14 to 15 hours before the test. The means for these separate experiments are 43.4, 43.3, and 37.0 minutes, based upon 34, 42 and 22 fishes, respectively. The lower value for the last lot is of highly probable significance, statistically speaking (only 2 chances in 10,000 that it is "accidental"), though it is not, of course, certain that this difference is due to their longer sojourn in the cool water (Cf. differences among the "Preston at Preston" lots, where no such explanation can be employed).

Somewhat disconcerting is the fact that the "Mormon at Preston" series as a whole showed a slightly *lower* mean resistance than the fishes which were native to the Preston Spring. This difference is of the opposite sign to that found by us in the comparable experiment in Ash Meadows (fig. 1). Moreover the difference is of rather probable significance ($3.7 \times$ P. E.). It is possible that transfer to water 15° C. lower (the difference at Ash Meadows was only 9°) resulted in a lessened resistance to cyanide, in the case of the Mormon Spring fishes, which outweighed the favorable effects of the lowered metabolic rate.

On the other hand, it seems possible that these differences between our results with *Cyprinodon* and with *Crenichthys* represent actual physiological differences between these two genera. In this re-

spect, comparison is interesting between our experiments and some recently reported for certain invertebrates (Fox, '36; Fox and Wingfield, '37).

(4) The low survival time of the "Preston at Mormon" series in comparison with all the others, including the "Mormon at Mormon" series, has already been pointed out. The superior resistance of the latter might be expected on the supposition that the resident fishes had, as a result of physiological adaptation, a lower metabolic rate than those which had been recently introduced from a lower temperature (Cf. Sumner and Doudoroff, '38). However, it would also be possible to interpret this lower viability of the introduced fishes as due to the cumulative effect of two lethal agencies, heat and cyanide. There is no doubt that even moderately high temperatures have a lethal effect upon fishes quite independent of their effect upon oxygen consumption.

In addition to the foregoing experiments, involving determinations of survival time in KCN, several tests were made of the more direct effects of transferring these fishes from cool to warm water and vice-versa.

(1) About 60 specimens of *Crenichthys* were taken from Preston Spring to Mormon Spring in two of the large bottles already referred to. The temperature of their water was raised in about ten minutes from 20.5° to that of the ditch in which they were placed in two screen cages (35.2°). On the following day, all of these fishes were dead, with the appearance of having been so for some hours.

(2) Twenty-four Preston Spring fishes were taken by bottle to Mormon Spring. The water in the bottle was immersed and warmed throughout a period of an hour to nearly the temperature of the spring. The fishes were then transferred to a screen cage in the outflow from the spring, at a point where the temperature was 36° and the oxygen content 2.09 ml. per liter. The majority of the lot were soon unable to right themselves in the water current and drifted helplessly against the sides of the cage. Within less than half an hour, one or two appeared to be dead; while in 1¾ hours all were dead.

(3) In contrast with the foregoing, 14 Mormon Spring fishes which had been kept in Preston Spring for 43 hours, and which had shown no unhealthy symptoms during that time, were brought to Mormon Spring and placed in another cage, alongside those discussed in the preceding paragraph. All of these were living and apparently well on the following day, after 24 hours at the higher temperature, with the exception of a single individual which had probably died early in the experiment. Thus a sojourn in the cool spring for nearly two days had not appreciably affected the adaptation of these fishes to the high temperature.

The death of the cold-spring individuals in warm water seems to have been due neither to the greatly reduced oxygen content of the latter nor to the heightened oxygen requirements of the fishes themselves. This is rendered probable by two circumstances: (1) the oxygen content, at the points where the experiments were actually performed, was nearly or quite as great in Mormon Spring as in Preston Spring; (2) fishes of the warm-spring population swim freely into the immediate vicinity of the point of outflow, and thus into water having an oxygen content not more than a sixth that of the stream a short distance below. Many fishes are known to be able to adjust themselves to widely different oxygen concentrations in their medium.

Summary

(1) Fishes (*Cyprinodon* sp.) inhabiting a warm spring, at 32.5°–33° C. were found to have, at this temperature, a mean survival time, in thousandth-molar potassium cyanide, only 64 per cent of that shown by individuals inhabiting a cooler spring (23.8°–24.0°) at the latter temperature. From this it is perhaps fair to infer that under natural conditions, the

respiratory metabolism of the fishes inhabiting this warm spring is more than one and a half times as high as that of those inhabiting the cooler spring.

(2) Fishes of another poeciliid genus (*Crenichthys*) inhabiting a considerably warmer spring (35.5° to 37.0°) were found to have a survival time less than a fourth (0.22) of that shown by individuals inhabiting a cool spring (21.0°), when each series was tested at its own habitual temperature. This seems to indicate for the former a metabolic rate four or more times that of the latter.[10]

Although in each of these cases, it is likely that the two contrasted populations have been separated for a long period, probably some thousands of years, and that the temperatures of their habitats have differed rather widely throughout this period, we must conclude that such physiological adaptation as may have occurred has not been sufficient to bring about any considerable approximation of these metabolic rates.

(3) Whether or not any physiological adaptation in respect to metabolic rate occurred, such that individuals of two contrasted populations would show measurably different survival times if tested under the same temperature conditions, is not altogether certain. *Cyprinodon* seemed to furnish some evidence for the existence of such a modification, when samples of the two populations were subjected to the cyanide test at the lower temperature. The converse experiment (testing the two populations at the higher temperature) was not performed with this fish. *Crenichthys,* on the contrary, failed to reveal any probable difference corresponding to that shown by *Cyprinodon*—indeed there was a slight difference in the opposite direction—when tested in the cooler water. The converse experiment, however, revealed a marked difference in resistance to KCN between the two respective lots, the cool-spring fishes, in warm water, succumbing considerably more rapidly than those native to the latter. As we have stated, however, this result is subject to another possible interpretation, not involving any assumptions respecting the relative metabolic rates of the two lots of fishes.

(4) Quite apart from any such problematic effects, in the direction of adaptation, upon the metabolic rate of these fishes, we have observed certain undoubted physiological differences between the warm-spring and cold-spring individuals. It was shown for *Crenichthys* that warm-spring specimens could be transferred to the cold-spring for two days (time did not permit of a longer test) and returned to the warm spring, without apparent harm, whereas specimens native to the cold spring were speedily killed by transfer to the higher temperature. Reasons were given for believing that the death of the cold-water fishes in warm water was due to other factors than the reduced oxygen content of the latter or the heightened oxygen requirements of the fishes themselves.

[10] Referring, of course, to the actual, not the potential metabolic rate, *i.e.,* to that maintained under the normal life conditons of each population.

Literature Cited

Fox, H. M. 1936. The activity and metabolism of poikilothermal animals in different latitudes. I. *Proc. Zool. Soc. London,* pp. 945–955.

Fox, H. M., and C. A. Wingfield. 1937. The activity and metabolism of poikilothermal animals in different latitudes. II. *Proc. Zool. Soc. London* **107**: 275–282.

Hubbs, C. L. 1932. Studies of the fishes of the order Cyprinodontes. XII. A new genus related to *Empetrichthys. Occas. Papers Mus. Zool., Univ. Michigan, No. 252:* 1–5.

Sumner, F. B., and P. Doudoroff. 1938. Some experiments upon temperature acclimatization and respiratory metabolism in fishes. *Biol. Bull.* **74**: 403–429.

Wales, J. H. 1930. Biometrical studies of some races of cyprinodont fishes from the Death Valley region, with description of *Cyprinodon diabolis,* n. sp. *Copeia* **1930** (3): 61–70.

Wells, N. A. 1935. The influence of temperature upon the respiratory metabolism of the Pacific Killifish, *Fundulus parvipinnis. Physiol. Zool.* **8**: 196–227.

Contribution No. 82

Reprinted from THE JOURNAL OF EXPERIMENTAL ZOOLOGY
Vol. 83, No. 2, March, 1940

FURTHER EXPERIMENTS ON THE RELATIONS BETWEEN OPTIC STIMULI AND THE INCREASE OR DECREASE OF PIGMENT IN FISHES [1]

FRANCIS B. SUMNER
Scripps Institution of Oceanography, La Jolla, California

FOUR FIGURES

For some years the writer and several collaborators have been experimenting upon the effects of visual stimuli on the production or loss of pigment in certain fishes. These experiments have been concerned with the influence of both light intensity and background, with the effects of these upon both melanophores and xanthophores, and with both the number of pigment cells and the quantity of pigment.

In the course of these experiments, our procedures have been changed from time to time, as likewise our mode of presenting the same data to the reader. Thus various apparent inconsistencies would be evident to a reader who should carefully compare the various reports of this work. It must be added, however, that our original conclusions have, for the most part, been confirmed by the later experiments. The most serious discrepancy relates to the position of our "black" background in the scale of albedos. This, on careful measurement, has been found to have a considerably lower value than had been assigned to it previously on the basis of a rough estimate.

In the first of our series of experiments (Sumner and Wells, '33), it was shown for Lebistes reticulatus that both the number of black pigment cells (melanophores) and the melanin content of the individual cells underwent large changes, in

[1] Contributions from the Scripps Institution of Oceanography, new series, no. 82. Services were rendered by various persons throughout these studies under W. P. A. Project 665-03-3-141.

opposite directions, in response to black and white backgrounds. No quantitative determinations were made, however, at this time, though numerous photographs were taken of stages in the multiplication or elimination of the melanophores.

Sumner and Fox ('35), found that in Girella nigricans the quantity of the yellow pigment xanthophyll might also be strongly influenced by the background on which the fishes were placed though, rather unexpectedly, it was the shade (whether light or dark) rather than the color, sensu stricto, which was influential in determining the quantity of this substance. While fishes became black upon a black background, and yellowish upon a yellow one, they accumulated much more xanthophyll in the former than in the latter. In the first case, however, the xanthophores were masked by melanophores.

Sumner and Doudoroff ('37, '38) undertook to determine the quantitative relations which might obtain between the amounts of melanin that could be extracted from the various lots of experimental fishes and the visual stimuli to which the latter had been subjected. This, of course, necessitated measurements of some accuracy both of the optical conditions involved and the melanin contained in the bodies of the animals. Fishes were kept in aquaria of several shades: black, white and two (later three) grays. Others were subjected to several widely different grades of illumination, in order that possible effects of light intensity could be studied independently of those of background.

These experiments seemed to show, among other things (1) that the melanin content of the fishes tended to be inversely proportional to the logarithm of the albedo of the background on which they had been kept; (2) that the intensity of the incident light, if influential at all, was a minor factor in determining the differences of pigmentation which were observed.

While the results of these experiments were highly suggestive, our experiences, particularly with the second series ('38) made it evident that we had not yet attained a really satisfactory method of assaying the melanin. Not only were

considerable differences found between samples of material which should have given identical values, but the same samples were found to undergo considerable alteration with the lapse of time. A change of method was clearly indicated. The procedure employed in the two latest experiments, here to be discussed, consisted in counting the melanophores in certain areas of the skin. For one region of the body, at least, it was found that the counting, though tedious, could be accomplished with fair precision.

The first of these experiments related to the effects of backgrounds. Five of these were employed: white, three shades of gray and black. Shallow jars or bowls of clear white glass were used as aquaria. These were 24 cm. in diameter and 15 to 17 cm. deep. They were painted on the outside with "Glyko" auto enamel of the required shades.[2] They were about half filled with fresh water, and covered with ¼-inch wire screen to prevent the fishes from jumping out. Fifteen of these aquaria were used, three of each shade. About thirty-five female specimens of the guppy (Lebistes reticulatus) were placed in each of the aquaria at the commencement of the experiment. Care was taken to distribute these as uniformly as possible according to size.

The conditions to which they were subjected, particularly the exclusion of water plants, were not favorable to the health of the fishes, and considerable numbers of these died in the course of the 2 months (64 to 65 days) of the experiment.[3]

Daphnia and a prepared fish food were supplied to the fishes, three times a week at first, later twice daily. In order to prevent serious discoloration of the backgrounds, food remains and feces were siphoned off every other day, and the bowls were washed once a week.

[2] These grays, while approximately neutral, proved to be slightly bluish. It should be pointed out, too, that the present grays do not correspond very closely in albedo with those of previous years.

[3] The cause of the mortality was a quite different disease from that described by Sumner and Doudoroff ('38 a) for Gambusia, and there was no differential death rate in relation to the background.

The water temperature during the period of the experiment ranged between 24.5° and 28°C.

The aquaria were kept in a cabinet divided into four compartments, each lighted by a 100-watt lamp in the ceiling and painted white within. Readings of the incident light made with a Weston "Foot-candle Meter" ranged from 30 to 32.5 foot-candles. For the purpose of these readings, the instrument was placed on the bottoms of the aquaria, the latter being empty of water but covered by the wire screen.

The determination of the albedos of the backgrounds—i.e., of the bottom and walls of the aquaria—was a matter to which much attention has been given.[4] By albedo is here intended the specific reflectivity of a given surface, i.e., the proportion of incident light which it reflects. It is, for example, all that makes the difference between a neutral gray and white.

The method here to be described differs altogether from that upon which the figures reported in our previous papers were based. Whereas previous determinations of albedo had been made upon strips of flat glass, sprayed with the various paints in question, and examined with the Ives Tint-photometer, the values here reported are based upon galvanometer readings of the current from a Weston photronic cell, exposed to reflections from the bottoms of the aquaria. An attachment was fitted to the photronic cell, consisting of (1) an iris diaphragm, provided with a scale, and placed at a distance of about 4 mm. from the disc of the cell; and (2), beyond this, a very short tube, ending in a window of thin glass. The whole was inverted and held in a clamp, the glass window being immersed in the water of the aquarium under examination, at a distance of 13 cm. from its bottom. Two 200-watt lamps were placed in the ceiling of the cabinet, as far apart as possible. The light reflected from the bottoms of the bowls was received in the photronic cell, which was

[4] I must here acknowledge the valuable assistance of Prof. L. M. K. Boelter and Mr. F. A. Ryder of the Department of Mechanical Engineering, University of California, of Prof. J. W. Ellis of the University of California at Los Angeles, and of Dr. R. T. Young, Jr., of the Worcester Polytechnic Institute.

connected with a sensitive mirror galvanometer (L. & N., no. 2500). The very great differences in the reflectivity of the different aquaria were compensated by adjustment of the iris diaphragm.

During these tests the sensitive disc of the cell "saw" much the same visual field that the fishes saw below them, including the points of high light, reflected from the curved and somewhat irregular surfaces of the aquarium bottoms. To complete the similarity of this set-up to that actually existing in the experiments, food debris and feces, in a roughly average amount, were scattered upon the bottoms of the aquaria in one of the series of light measurements, and it is this series which has been used in the present calculations. This procedure raised very appreciably the readings from the black, and lowered those from the other backgrounds, particularly from the white. Several (usually five) different apertures (diaphragm adjustments) were employed with each background, and the ratio of the galvanometer reading to the area thus exposed was computed for each of these. This ratio was approximately constant for each background, though tending to increase somewhat with the size of the aperture.[5]

The values of albedo obtained in this way are only relative ones. The actual percentages of the incident light which were reflected by these various bottoms could not be computed without my having accurate measurements of this incident light, made beneath the water in the aquaria, and such measurements would be difficult to make. However, it is simple enough to compute the values relative to "white," regarded as 100%, and these are the values which are here chiefly required.

These relative values, both with and without food debris, etc., on the bottoms of aquaria, are given in table 1.

It is the figures in the second column which have been used in our present computations. The low value obtained for the black aquaria was surprising, in view of the pale debris on the bottom and the points of high light, due to re-

[5] Allowance has been made by the writer for the considerable fluctuations which may occur in the sensitivity of these photronic cells.

flection from the glass. Our previous crude estimate of this value, made in the absence of any exact photometric measurement, was 2.0 (±) (Sumner and Doudoroff, '37; Sumner, '39).[6]

In the second experiment here considered, it was my object to test more precisely the part which was played, if any, by light intensity in influencing the production or elimination of melanophores. The four compartments of the cabinet were lighted, respectively, by a 200 watt lamp (clear), 40 and 10 watt lamps (frosted), and a 7.5 watt lamp, placed within a translucent white globe. The actual light intensities, measured beneath the screens covering the aquaria were approximately 64, 5.3, 0.85 and 0.24 foot candles, respectively.[7]

TABLE 1

	BOWL WASHED	WITH DEBRIS
White	100.00	100.00
Pale gray	35.84	42.92
Medium gray	13.03	16.38
Dark gray	6.17	8.36
Black	0.38	0.74

The ratios between each of these and the next lower grade of illumination are 12.0, 6.2 and 3.5, respectively. Thus the most brightly lighted fishes received about 265 times as much light as the least brightly lighted ones.

Because of marked differences in the heating capacities of these lamps, special steps were necessary in order to keep the temperatures of the four compartments approximately equal. The greatest difference between the mean temperatures of any two of these was 0.3°C.

Although the object of this experiment was to test the effect of light intensity rather than that of the albedo of the

[6] Flat strips of clean black-painted glass gave a tint photometer reading of 0, but this obviously did not represent the visible background of the fishes kept in the black bowls.

[7] Owing to certain differences in the conditions, these values differ from ones previously reported for similar series of lamps.

background, two different backgrounds, black and medium gray, were employed in each of the compartments.

More than 500 female guppies were distributed to the sixteen aquaria here employed. Owing to conditions already mentioned, more than a fourth of these fishes died before the conclusion of the experiment, just 6 weeks later.

The methods of preparing the fishes and of counting the melanophores which were employed in these two experiments were almost identical. The fishes were (1) subjected for 1 hour to a 1:4000 solution of adrenalin, in order to bring about the concentration of the melanin granules, a condition which greatly facilitates the counting of the melanophores. They were (2) fixed in sublimate acetic; (3) washed in alcohol; and (4) decalcified in acidified alcohol ($2\frac{1}{2}\%$ nitric acid). After washing off partially, (5) the acid was neutralized with $CaCO_3$. The fishes were (6) transferred to absolute alcohol (1 day); then (7) to cedar oil, where they could be kept indefinitely, pending the counting of the melanophores.

Immediately before this last procedure, each fish was measured to the tenth of a millimeter with a dial caliper. Individuals under 20 mm. in length were excluded from the series. The fish was next laid upon a flat surface of cork and cut as follows with a safety razor blade: (1) a horizontal slice was taken from the anterior dorsal surface, commencing just below the mouth and extending back to the anterior end of the dorsal fin; (2) a portion of the posterior region of the body was detached by a cross-cut well in advance of the caudal fin.

The former of these two pieces included the "upper lip" (premaxillary region). Those cells were counted here which fell within a particular row of squares in a Whipple eye-piece micrometer disc, the specimen being so oriented as to bear a consistent relation to the grating of the micrometer (fig. 1). After considerable examination of the material, it seemed probable that the melanophores of this region of the body were the most suitable ones for counting with a fair degree of accuracy.

Figures for the other area of skin in the caudal region, were on the whole much less reliable. They were further complicated by the fact that in specimens from the darker backgrounds, particularly from black, numerous very small specks of pigment appear in the more superficial layer of the dermis. It is clearly misleading to give these minute specks of melanin, not always even identifiable as melanophores, a rating equal to that of masses many times their size. Yet the two classes intergrade so completely that it is impossible to exclude any of them.

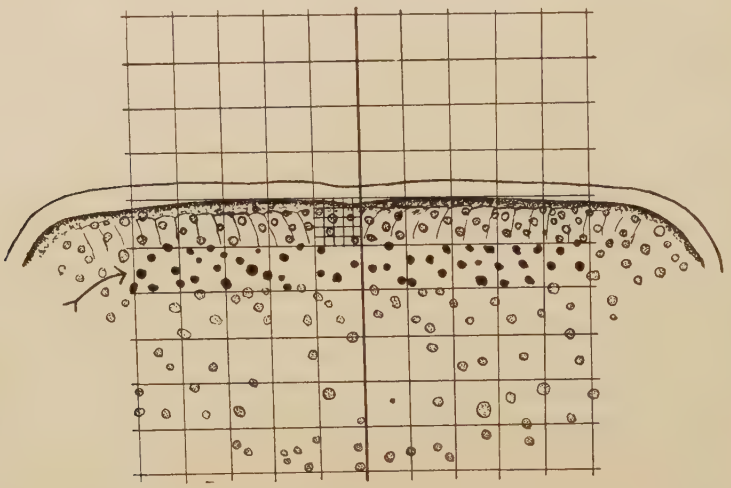


Fig. 1 Melanophores of the premaxillary region (''upper lip'') of Lebistes, the arrow indicating the column selected for counting in experiment 1 (melanosomes in solid black). (In experiment 2, the area was slightly farther back.)

During the counting of the melanophores, the specimen was placed in a special glass cell, filled with cedar oil. The counting was usually a simple process, and repetitions made after considerable intervals usually checked the original ones very closely.

Table 2 comprises figures for the mean body length and the mean number of chromatophores in both the premaxillary region and the caudal region of fifty fishes from each of the five backgrounds employed in the present experiment.

Figure 2 consists of histograms depicting the frequency distributions of the "premaxillary" values for each of the five lots of fishes comprised in experiment 1. It is probable that the immense variability within each of these lots is due largely to genetic differences in a highly mixed stock of Lebistes. Despite this variability, however, the trend shown by the series as a whole is unmistakable.

The mean differences in melanophore number among these various lots of fishes are considerable. They are not, however, nearly as great as might have been expected from the appearance of the animals when alive. While, for example, those from the black bowls were certainly many times as black as those from the white, the number of chromatophores in the premaxillary region is less than three times as great.

TABLE 2

	LENGTH	PREMAX.	CAUDAL
White	24.9	23.88	12.78
Pale gray	25.3	33.48	21.45
Medium gray	26.2	39.48	24.39
Dark gray	26.1	49.78	40.65
Black	25.9	60.98	76.54

The broad overlapping of the frequency distributions of the various lots is likewise surprising in view of the pronounced mean differences in the appearance of these lots when living. It is evident that a large part of the visible difference of shade among these fishes is due to factors other than the number of melanophores. Some of it is due to the melanin content of the individual melanophores, much of it, of course, to the state of aggregation or dispersion of the melanin.

Figure 3 is based upon the mean values of the five series represented in figure 2. It shows the relations between the number of melanophores per unit area of the upper lip and the albedo of the background on which the fishes had been kept. The albedos (abscissas) have been reduced to percentages of the albedo of the white background, taken as 100 (table 1). The numbers given for the melanophores (ordi-

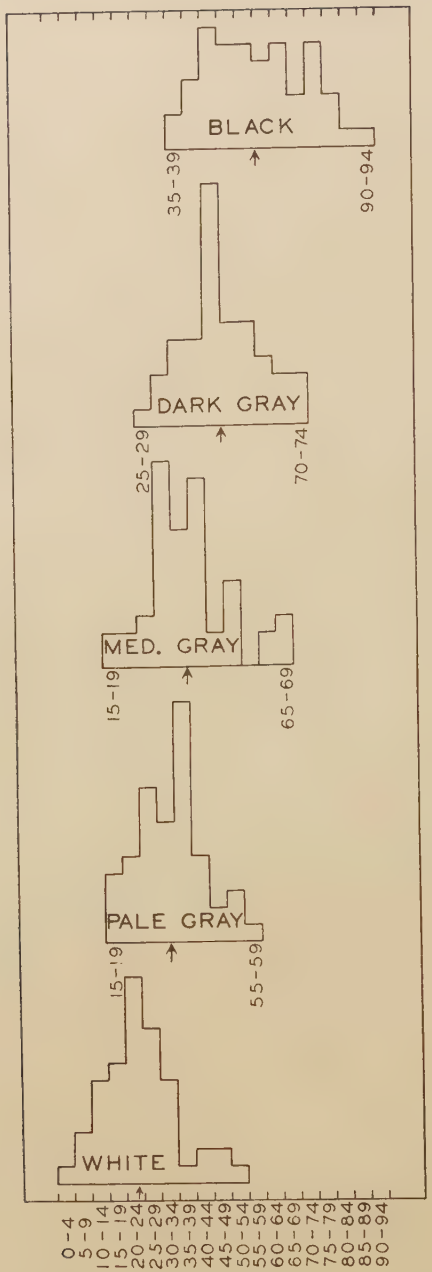


Fig. 2 Frequency distributions of the number of melanophores in a definite area of the skin of Lebistes (shown in fig. 1). Based upon fifty individuals from each of the backgrounds, including the twenty-five comprised in figure 3 of Sumner ('39).

nates) are multiples of the mean number for the "white" fishes, taken as unity (1.00, 1.40, 1.65, 2.08, 2.55). The curve here plotted is closely similar to that published by Sumner and Doudoroff ('37, fig. 3, "series A") for measurements of melanin, and by Sumner ('39, fig. 4), for the first twenty-five specimens of the series with which we are here dealing. Further comparisons of these figures will be made later.

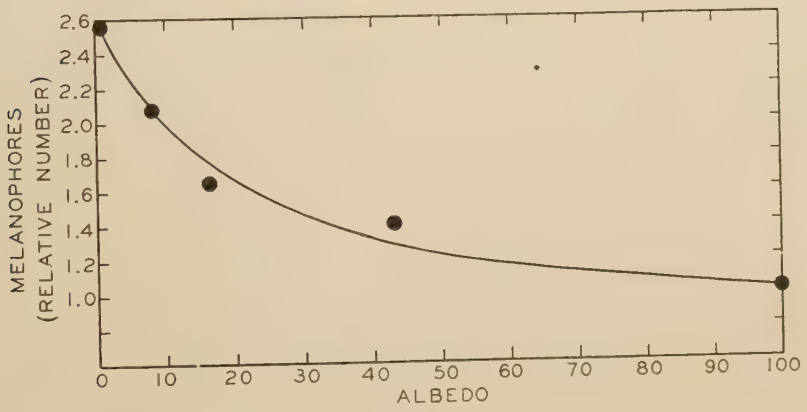


Fig. 3 Abscissas: albedos of the five backgrounds, taken as percentages of that of "white," regarded as 100. Ordinates: mean values of the five lots of fishes included in figure 2, reduced to multiples of the mean value for the "white" fishes.

The form of this curve suggests a logarithmic relation between the two sets of values. Figure 4 shows that this relation holds fairly closely for all of these lots of fishes with the exception of those from black. It would be necessary either to raise the albedo from 0.74 to about 2.0, or to raise the melanophore index from 2.55 to about 3.0 in order to bring the "black" fishes into line. It is plain, however, that the relation between the two variables, albedo and melanin production, is much more nearly a logarithmic than a linear one. The logarithmic relation, though not as perfect as we had supposed, may still be regarded as an approximate description of the facts. This subject will receive further attention later (p. 342).

That the number of melanophores in an equal area of skin would vary with the age (size) of the fish might perhaps have been expected. Table 3 gives the mean figures for all the size classes comprised in experiment 1, each based upon the unweighted means of the separate means for the five series of fishes (white, pale gray, etc.). Some positive correlation

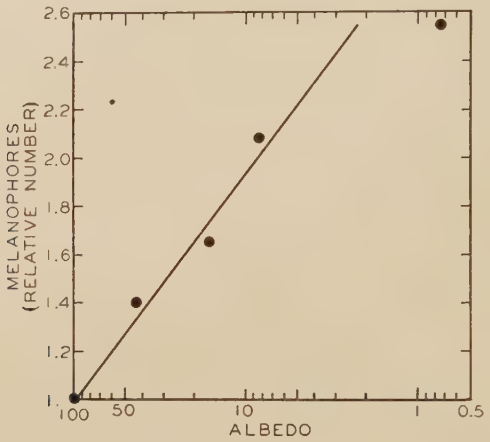


Fig. 4 Same values for melanophores as in figure 3, plotted against the logarithms of the albedos.

TABLE 3

SIZE GROUP	NUMBER OF INDIVIDUALS	MEAN NUMBER OF MELANOPHORES
20–21	17	35.8
22–23	60	39.2
24–25	66	43.1
26–27	56	42.7
28–29	32	43.1
30–	19	46.4

would seem to be indicated between size and the abundance of melanophores in the given skin area, though this does not hold throughout all of the size classes. It is important to record that separate graphs, not here reproduced, make it plain that the populations of the different types of aquaria stand well apart from one another, regardless of the size of the fishes.

The relations shown by the melanophores of the caudal region (table 2) are not very instructive for reasons already given. As previously stated the numbers obtained on "black" and to a lesser degree for "dark gray" are not comparable with those for the other aquaria.

The second experiment of the 1939 series was concerned primarily with testing the possible effect of light intensity upon melanophore production. The results of this experiment are summarized in table 4. The figurers for melanophores are those for the premaxillary region ("upper lip"). Comparison with the corresponding figures in table 2 shows at once that these later figures, particularly those for black,

TABLE 4

LIGHT INTENSITY (FOOT CANDLES)	BLACK			MEDIUM GRAY			MEANS OF MEANS (BLACK AND GRAY) MELANOPHORES
	No.	Body length	Melanophores	No.	Body length	Melanophores	
0.24	40	25.3	44.25 ± 1.03	32	24.8	33.62 ± 1.46	38.93
0.85	41	23.9	43.78 ± 0.84	36	23.8	34.14 ± 1.52	38.96
5.3	29	24.4	48.34 ± 1.42	33	24.3	34.21 ± 1.25	41.27
64.0	38	23.9	46.42 ± 1.27	27	23.9	39.74 ± 1.56	43.08
Means (unweighted)		24.39	45.70		24.20	35.43	

are much lower than the earlier ones. This is probably due to two circumstances: (1) the experiment was continued for a briefer period (6 weeks instead of 2 months); (2) a somewhat different area of the upper lip was selected for the melanophore count.[8] Owing, it is probable, to the first of these circumstances, the ratio of melanophores of the "black" fishes to those of the "medium gray" ones was here 1.29:1, while in the earlier series it was 1.54:1.[9]

Of chief interest is the last column in the table. It might appear from this that there is a steady, though slight increase

[8] This was done because of the somewhat different contour of the head of many of these specimens in comparison with those of the earlier series.

[9] It is true that the conditions of illumination in the two experiments were different, but this fact probably affected the issue very little.

in pigmentation with the intensity of the illumination. However, there is little consistency in this respect when the figures for the two backgrounds are compared. Whereas for gray, the first of the figures is the smallest and the last the largest, for black the second is smallest and the third the largest. Moreover, no single difference is as much as three times its probable error, and most of them bear a much smaller ratio.

However, if we grant the reality of the differences shown in the last column, we find a mean total increase of 10.8% when the last figure is compared with the first. This represents the effect of increasing the incident light some 265 times (p. 332). In comparison with this (table 2) we have a decrease of 61% in the number of melanophores when we pass from black to white, or conversely, an increase of 155% when we pass from white to black. This represents, as we have seen, a 135-fold change in albedo (table 1, second column). It is obvious that changes in albedo are many times more effective than changes in light intensity in bringing about changes in the number of melanophores. Whether we are warranted in assigning a definite value to this difference in the potency of the two factors (either elevenfold or twenty-eightfold), on the basis of the foregoing figures, seems questionable.

Incidental, only roughly quantitative determinations were made of the effects of these various optical conditions upon the xanthophyll content of the fishes. Striking differences were noted in the color of the 95% alcohol to which the fishes were subjected at one stage in their preparation (p. 333). In the first of the foregoing experiments, in which five backgrounds were used, it was obvious that the alcohol from the "black" fishes was by far the most highly colored (yellow) of any from this series, while that from the "dark gray" ones rated second. The other three lots did not differ from one another appreciably in this respect.

In the second experiment, the extracts from the "black" fishes were more deeply colored than those from the "medium gray" ones at all four intensities of illumination, the latter

factor having little or no influence in the matter. In comparisons made with Nessler tubes it was found necessary to dilute the xanthophyll solution from "black" fishes to 25% the strength of that from "gray" fishes in order that the two should approximately balance. Since the weights of the two lots of fishes (roughly equal) were not taken, nor the xanthophyll completely extracted, these determinations cannot be regarded as precise (compare Sumner and Fox, '35).

SUMMARY AND DISCUSSION

The present paper reports the results of two experiments with the guppy (Lebistes reticulatus), both concerned with the quantitative effects of visual stimuli upon melanophore production (or loss). In the first of these, the fishes were exposed for 2 months to backgrounds of five shades: black, white, and three grays, all of these being nearly equally lighted from overhead. In the second experiment, the fishes were subjected for 6 weeks to four grades of illumination, the brightest of these having about 265 times the intensity of the dimmest. Incidentally, two types of background (black and medium gray) were employed with each of these degrees of illumination.

Much more precise methods were employed than in our previous experiments for measuring both the intensity of illumination and the albedos of the backgrounds.

In each case, the effect of the experimental conditions upon the production or loss of melanophores was determined by counting the number of these in a definite area of the skin.

The results of these experiments agree essentially with those previously reported for Gillichthys and Gambusia, although in the case of these last fishes we were dealing with measurements of the quantity of melanin rather than with counts of the melanophores.

1. The fishes responded to the background in such a manner that the number of melanophores tended to vary inversely as the logarithm of its albedo.

2. The intensity of the incident light had little if any effect upon the number of melanophores.

As regards the first of these conclusions, one important reservation must be made. The proportionate number of melanophores in the "black" fishes is considerably short of that required to maintain the stated relation to the background. With an albedo of 0.74% (of the "white") it would be necessary to raise the melanophore index from 2.55 to about 3.0 in order to bring the "black" fishes into line. However, the discrepancy between the pattern shown in figure 4 of the present paper and a recently published graph based upon a portion of the same material (Sumner, '39, fig. 5) is not due to any considerable revision of the relative positions of the five series of fishes. It is due to a considerable lowering of the value which must be assigned to the albedo of the "black" background, on the basis of careful instrumental measurements. It is unfortunate that I neglected, in presenting this graph in the earlier paper, to emphasize the fact that the value therein assigned to black was merely a crude estimate. I trust that the reader will bear in mind that the figure herein presented (fig. 4) supersedes the earlier one.[10]

This relatively low value for the melanophores of the "black" fishes, as well as that for the melanin of the latter in the earlier (Gillichthys) experiment has a possible theoretical interest. The analogy has already been pointed out (Sumner and Doudoroff, '37; Sumner, '39, '39 a) between these pigmental relations of fishes and those phenomena of human sense-perception upon which the "Weber-Fechner Law" was based. As is well known, this "law," so far as it relates to visual stimuli, breaks down in the realm of feeble intensities, greater relative increments of stimulus being required in order to bring about perceptible increments of sensation. Whether

[10] A few word of emendation are also desirable regarding figure 3 in Sumner and Doudoroff ('37). The abscissas there given were based on an attempt to determine the true albedos of the various backgrounds. It is a much safer procedure to state these as percentages of the white background, as has been done in the present paper. Incidentally, I will point out a misprint on the second line of the text below this figure. "6.3" should read "2.3."

this deficient (even if actually very high) production of melanin upon a background of very low albedo can be regarded as comparable with the human case is, of course, far from certain.

Respecting the second of the main conclusions from these experiments—the relative ineffectiveness of light intensity within the ranges here employed—I need only repeat that this conclusion is in harmony with results previously reported for the measured melanin content of the body in Gillichthys. As in the present case, higher illumination seems slightly to favor melanin production, though in neither case is the difference statistically certain.

The amount of xanthophyll accumulated by these fishes was likewise found to vary with the albedo, being markedly greater in ones from the darker backgrounds. No very precise determinations were made, however.

LITERATURE CITED

(A much more comprehensive bibliography of this field has been presented in a previous paper (Sumner, '39).)

SUMNER, F. B. 1939 Quantitative effects of visual stimuli upon pigmentation. Am. Nat., vol. 73, pp. 219–234.

———— 1939 a Human psychology and some things that fishes do. Sci. Monthly. September, 1939, pp. 245–255.

SUMNER, F. B., AND P. DOUDOROFF 1937 Some quantitative relations between visual stimuli and the production or destruction of melanin in fishes. Proc. Nat. Acad. Sci, vol. 23, pp. 211–219.

———— 1938 Some effects of light intensity and shade of background upon the melanin content of Gambusia. Proc. Nat. Acad. Sci., vol. 24, pp. 459–463.

———— 1938 a The effects of light and dark backgrounds upon the incidence of a seemingly infectious disease in fishes. Ibid., pp. 463–466.

SUMNER, F. B., AND D. L. FOX 1935 Studies of carotenoid pigments in fishes. II. Investigations of the effects of colored backgrounds and of ingested carotenoids on the xanthophyll content of Girella nigricans. J. Exp. Zool., vol. 71, pp. 101–123.

SUMNER, F. B., AND N. A. WELLS 1933 The effects of optic stimuli upon the formation and destruction of melanin pigment in fishes. J. Exp. Zool., vol. 64, pp. 377–403.

Contribution No. 83

[From American Journal of Science, Vol. 238, Apr., 1940, Pp. 272-285.]

SAND MOVEMENTS ALONG THE SCRIPPS INSTITUTION PIER.*

FRANCIS P. SHEPARD and EUGENE C. LaFOND.

ABSTRACT. Discussion is presented of the results obtained from 600 repetitions of soundings along the Scripps Institution pier. The changes in sand level occurring at differing seasons of the year and accompanying various conditions of the sea are correlated with records of a current meter, a tide gauge, a wave-recording machine, and weather bureau instruments located on the end of the pier. The data show that sand cut away from the beach and foreshore during the stormy winter is deposited largely within 1,000 feet of the shore and is returned landward during the calm seas of the succeeding summer. The relation to cut and fill of various types of waves, of spring and neap tides, and of changes in current direction are all clearly demonstrated from the records.

INTRODUCTION.

IT has been known in a general way that waves, tides, and currents move sand along the shore and carry it in and out according to their character. However, up until the present investigation no comprehensive long range studies had been made to find out the exact nature of these movements and the degree to which the various factors were involved. The Scripps Institution of Oceanography at La Jolla, California, with its 1,000 foot pier extending out into the open ocean presented a unique opportunity to investigate these problems. Preliminary daily observations of the sand height on a rock face near the pier made in 1934, indicated the tidal and seasonal cycle of fill and cut of the beach. Beginning in 1936, measurements were taken from the deck of the pier to the sand at 45 equally spaced stations about once a week for two years; twice a week for one year; and daily for one year, October, 1937, to October, 1938. In addition, for one 28-hour period, measurements were made every 40 minutes along the entire length of the pier.

This work has been coördinated with many other observations. Almost continuous data have been available from the Coast and Geodetic Survey tide gauge and from the Dahl-Sverdrup current meter both located at the end of the pier. Wave heights were estimated from a tide staff at first, but beginning in 1938 a wave-recording device was installed for daily readings.

* Contribution from the Scripps Institution of Oceanography. New Series No. 83. Assistance in the preparation of these materials was furnished by the personnel of the Works Progress Administration Official Project No. 665-07-3-141.

The recording drum and reduction gears of the machine developed to record the character of the waves at the Scripps Institution pier.

Scripps Pier is located off the sea wall of the Scripps Institution and extends out from a beach of fine sand. Along the straight coast north of the pier a series of marine cliffs of Eocene sandstone and conglomerate rise to a height of 300 feet and extend as far as Torry Pines State Park which is four miles up the coast. To the south there are low cliffs cut into soft silts and alluvial sands of recent age. These extend for half a mile where they merge into a low plain, which formerly consisted of a sand bar built across a lagoon, but the lagoon has now been filled. This lowland also extends for half a mile and is terminated by more cliffs which rise near the bend in the coast at the head of La Jolla Bay.

Outside the pier at a distance of 3,000 feet is a submarine canyon which runs diagonally to the coast. Another canyon extends in almost to the beach a mile south of the pier. The sand along the pier, however, is not directly influenced by the canyon since the sloping bottom which extends along the pier is not terminated by the canyon but is bordered by a narrow 20 fathom terrace which separates this slope from the canyon. No doubt the presence of La Jolla Bay to the south and of the row of cliffs to the north exert a greater influence on sand movements.

ACKNOWLEDGMENTS.

The writers are indebted to C. I. Johnson for his help to LaFond in designing and for constructing much of the equipment used in this study. Appreciation is also expressed for the careful measurements and plotting work performed by K. D. Langley, K. O. Emery and R. S. Dietz.

PIER EQUIPMENT.

Sounding Machine.

The sounding machine consists of a ten-foot boom which rests on the pier railing and can be rolled along the dock and rail of the pier sounding for a distance of 900 feet. Paying over the end of the boom is a graduated piano wire which supports a 15 pound weight. The machine allows the taking of soundings at the 45 stations in a period of approximately half an hour. The machine is light enough so that it can be changed from one side of the pier to the other. By taking soundings half way between pier pilings and out ten feet, a distance of 14 feet

is maintained from obstructions which would set up special conditions.

Wave Recording Machine.

In order to record the heights of waves which pass under the end of the pier, a drum is allowed to float on the water guided in a vertical plane by two wires. Its up and down movement is recorded by means of an attached wire, connected through reduction gears to a moving arm which in turn records the character of the waves on a rotating cylinder (Plate I). Ordinarily this machine is run every day for a period of five to 15 minutes.

Dahl-Sverdrup Current Meter.

Near the end of the pier a current meter with an electrical recording device is kept in almost continuous operation. The current was determined for a level of approximately eight feet below mean sea level. Both speed and direction of the current are recorded on a continuous tape which is located in the laboratory on the end of the pier. This current meter was devised by O. Dahl and H. U. Sverdrup.[1]

Other Equipment.

In connection with other studies a rain gauge and anemometer are maintained on the pier. The records from these sources were consulted when looking for causes of beach and long shore changes. The direction of the wind was observed in connection with the daily anemometer reading. The pier is also used by the U. S. Coast and Geodetic Survey as a permanent tidal station. A tide gauge is maintained in constant operation and hourly records from this were obtained for tidal curves and for determining mean sea level.

NATURE OF SAND CHANGES.

Profiles have been made from most of the sand measurements along the pier. In order to show daily changes each new profile was plotted along with the profile of the preceding day. In this way it soon developed that there were large and rapid shifts in sand going on along the pier. When continuous soundings were made for a 28-hour period it was even found that there were appreciable shifts taking place during intervals as short as 40 minutes.

[1] Sverdrup, H. U., and Dahl, O.: Two oceanographic current recorders designed and used on the "Maud" Expedition. Jour. Optical Soc. Amer., Vol. 12, pp. 537-45, May, 1926.

The shifting of the sand was found to be particularly great in the breaker zone where, during 24 hours, a change of as much as 3.2 feet was observed. While the majority of these large changes were of the nature of cutting, the largest change on record was due to a fill.

Seasonal Changes.

In order to obtain a clearer idea of changes that were taking place along the pier, the sand heights at several stations were averaged together and plotted by groups. By this means the seasonal trend of the sand was determined for different zones. Interesting features became apparent from the plotting of these trends. Thus it can be seen from Text Fig. 1, that at stations 1—4, which are most of the time all above mean sea level, the sand undergoes a single major cyclic change during the course of a year which, however, has numerous smaller cycles superimposed upon it. Looking at the mean for stations 36—45, about 700 to 900 feet from the coast line, it can be seen that a less regular cycle has taken place during the year. During the spring months when the sand was lowest at the near shore stations it was highest near the outer end of the pier, and in the fall, when the sand had reached its highest level along the shore, it was reaching its lowest level around the pier end. Also, further examination will show that times of active cut near shore were generally times of active fill outside. This is particularly true in the fall months. Observing the mean for stations 21—30, which represent half way stations, it can be seen that a somewhat intermediate action has taken place, with, however, the greatest oscillation occurring during the time when the shore stations had reached low marks and the outer stations had reached their high marks. It will be observed that during the winter and spring the changes in all three of these zones were of a rapid and fluctuating character. On the other hand, in the summer and early fall the changes both inside and outside were gradual and consistent in their direction. During this same time the mid pier stations showed very little variation, being situated near the node of the sand shift.

Relation to Waves.

Comparing these seasonal changes along the pier with the daily record of maximum swells (Text Fig. 1), we find numerous points of correspondence. In the first place, it is perfectly clear that the period of greatest cut inside and greatest fill out-

side is closely related to the season of largest waves. Conversely, the period of shore fill and pier end cut is associated with months of very small waves. Exceptions to these rules will be noted, such as the most striking cut along the entire length of the pier on the second of May, due to the exceptional size of the waves, which were larger than any recorded along the pier before or since.

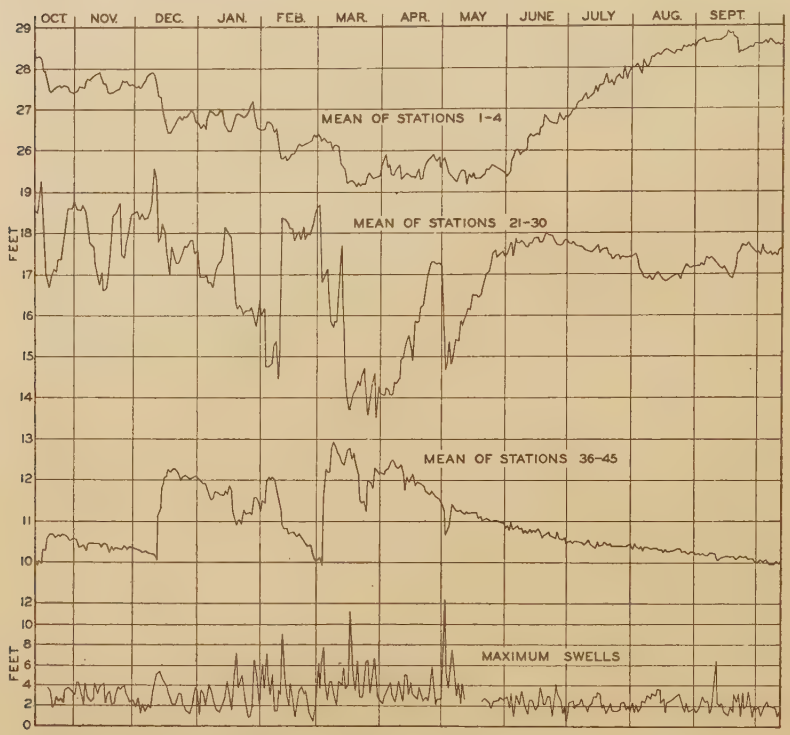


Fig. 1. The daily changes in the sand level for a year along the inner, middle, and outer sections of the Scripps Institution pier. Also the height of the maximum recorded waves for the same period.

It was found that the waves in this region averaged around three feet in height and have an average period of about nine seconds (Text Fig. 2, sec. A). In order to show the effect of various types of waves, profiles have been constructed which show the average daily change in sand height produced along the pier by waves of different size and period. The curves were selected for days with maximum waves between seven and 12 feet high (Text Fig. 2, sec. B), waves of 3.0 foot height with

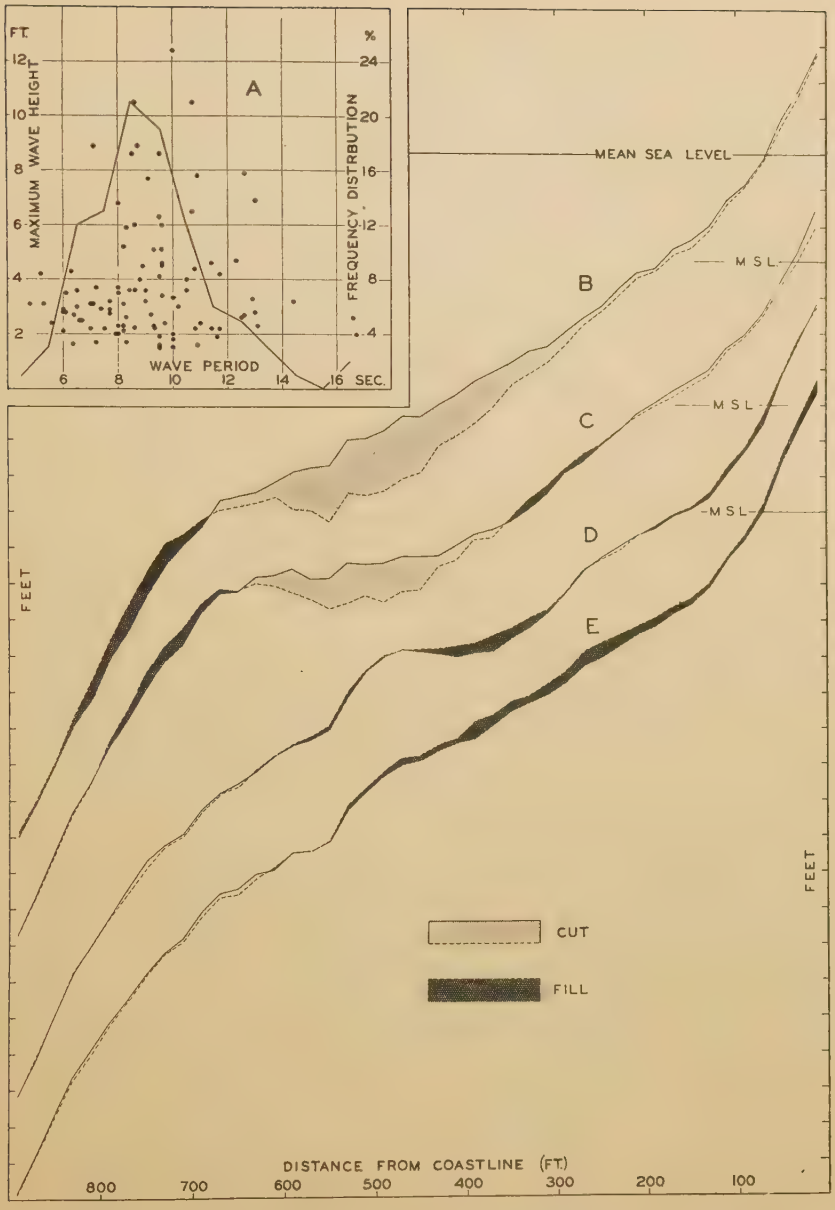


Fig. 2. (A) Maximum wave height plotted against wave period, represented by dots, and the frequency distribution represented by the solid line; (B) the average change in bottom profile during the first day of very high waves; (C) during three days of long period waves; (D) during three days of short period waves and, (E) during one week of low amplitude waves.

periods of over 11 seconds, (Text Fig. 2, sec. C), waves of 3.0 foot height with periods of about six seconds, (Text Fig. 2, sec. D), and waves of less than 2.5 foot height (Text Fig. 2, sec. E).[2] From these curves it will be seen that the large waves produce a considerable cut in the central part of the pier and a less pronounced fill outside. The average size waves with long period resulted in a similar but smaller change in profile. The average size waves with short periods, on the other hand, were followed by very small changes although rather appreciable fill in the middle and inner sections. The small waves were accompanied by still larger fill inside and a small amount of cut along the

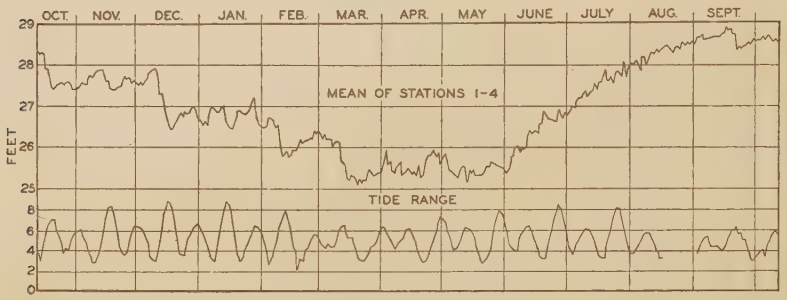


Fig. 3. The relationship between the changes in sand height along the inner pier zone and the range of the tide. High points on the lower curve represent spring tides and low points neap tides.

outer pier. These results show that both the size and period of the waves have important effects on the sand movements. Also, the waves of short period appear to act in the same way as waves of longer period and smaller size. Probably the failure of some fairly large waves to cut, and the large cutting of some waves of moderate size, can be explained to a considerable extent in this way.

Effect of Tidal Variation.

The sand level is shifted not only by the daily change of tide, which shifts the zone of breakers towards and away from shore, but is affected more markedly by the change from spring to neap tides. Ordinarily there are two highs and two lows each day. The tide range is obtained by taking the difference be-

[2] LaFond, Eugene C.: "Sand Movements Near the Beach in Relation to Tides and Waves." Submitted for publication in Proceedings of the Pacific Science Congress, 1939.

tween the higher high and lower low of the day. When the tide range is plotted with respect to time the neap tides appear as troughs and spring tides as crests. Comparison of the tide range for the year with the changes in stations 1—4 shows that there is some correspondence between the two, particularly from October till the large fill along the shore in June (Text Fig. 3). During this period the spring tides are almost invariably accompanied by a cut and the neap tides by a fill on this inner part of the beach. The relationship is, of course, obscured by the effect of the waves, but the tide appears to have fully as important an effect as the waves at these stations.

The influence of the tide is shown much better by plotting the changes at single stations where the greatest influence was felt. Thus in Text Fig. 4 we have chosen stations 1 and 6, which were located respectively at about 1.5 feet above mean sea level, and about 2.5 feet below mean sea level at this time of year. In order to neutralize the effect of other short period influences such as large waves, etc., each point on these curves showing sand level was made by averaging the day's observations combined with the two preceding and the two succeeding days. Examining the resulting curves we find that during April and May the sand at station 1 receives a maximum fill about two or three days after each neap tide, and a maximum cut about two or three days after each spring tide. Conversely, the sand at station 6 shows its maximum fill shortly after spring tides and its maximum cut shortly after neap tides. This, of course, suggests that sand had been moving back and forth between these stations according to the range of the tide.

Considering the changes in June we find that after the early part of the month the cut-fill relationship at station 1 ceases to conform with the tides and even some fill occurs during the spring tide. However, if we bring the record from station 2, which is 20 feet farther out, into the picture at this time (Text Fig. 4) we find the former correspondence of fill with neap tide and cut with spring tide. The explanation for this situation seems to be that by the tenth of June station 1 had been so filled that it ceased to have the proper relation to the sea level, and that station 2 had assumed this position. Stations which are several feet above mean sea level are likely to show fill instead of cut during the spring tides, partly because the waves carry sand far up the beach and the water sinks into the sand leaving the load behind. It may be seen, therefore, that measurement at one station along the beach or even the

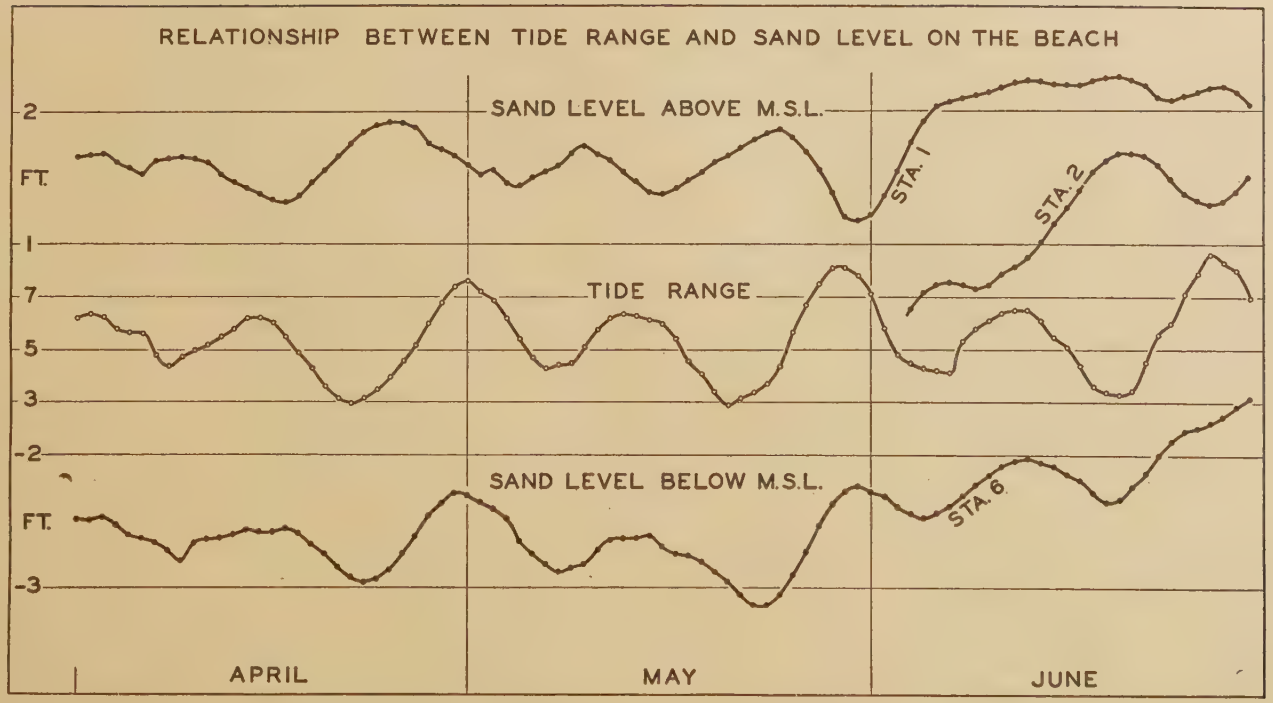


Fig. 4. Illustrating the effect of spring and neap tides on stations located approximately 1.5 feet above mean sea level and 2.5 feet below sea level.

grouping of several stations may fail to show the same relationship to spring and neap tides continuously throughout the year. However, by shifting the stations so as to keep them in the proper relationship to mean sea level, a correspondence can be shown throughout the year which is as good as in Text Fig. 4, except perhaps in July and August. Since the latter are, in general, the two months of greatest fill along the beach, it seems possible that the operation of this bi-weekly sand cycle may be partially obscured during this period of most rapid fill.

Relation to Grunion Runs.

The grunion spawning which takes place on this beach shows a remarkable correspondence to the curve of stations 1—4, (Text Figs. 3 and 5). The grunion deposit their eggs two and a half to three inches under the sand on the beach near the high tide level just before a period of fill so that the eggs become more deeply covered thus allowing them time to mature.[3] If the sand is removed in about two weeks the eggs are mature enough to hatch and the young go out to sea. The grunion choose April, May, and June as their chief spawning months when the tidal cycle is still in effect and when the sand has been cut to its lowest level, at least in April and May of 1938, so that neither seasonal cut nor fill will interfere with the process. It can be seen from the curves that no other months would serve these purposes as well.

Effect of Currents.

The relation between the currents and sand level can be shown best by a diagram showing both speed and direction. Since the currents are almost always to the north or south, parallel to the shore, the graph (Text Fig. 5), shows the resultant north or south current. It will be observed that currents to the south are more common. The record is not quite continuous because of occasional difficulties arising due to the meter being located relatively near the breaker zone.

Comparing the current record with the changes in the mean sand level of all the pier stations (Text Fig. 5), a rough correspondence may be observed. Generally, currents to the north are either accompanied or followed by fill, while currents to the south are generally accompanied or followed by cut. Also, it

[3] Thompson, Will F.: assisted by Julia Bell Thompson. "The Spawning of the Grunion." Fish Bull. No. 3, State of California Fish and Game Commission, 29 pages, 1919.

appears that the time of fill in the late spring and summer is a time of rather small currents. One of the cases where currents appear to be especially important is in February where a general cut along the pier is interrupted during a series of days of north flowing current, by a fill which lasted for about a month. The strongest north flowing current, which occurred in the middle of April, was followed by a fill that was distinctly ahead of the average seasonal trend. Still more significant, the three strongest south flowing currents correspond with the three largest cuts along the pier.

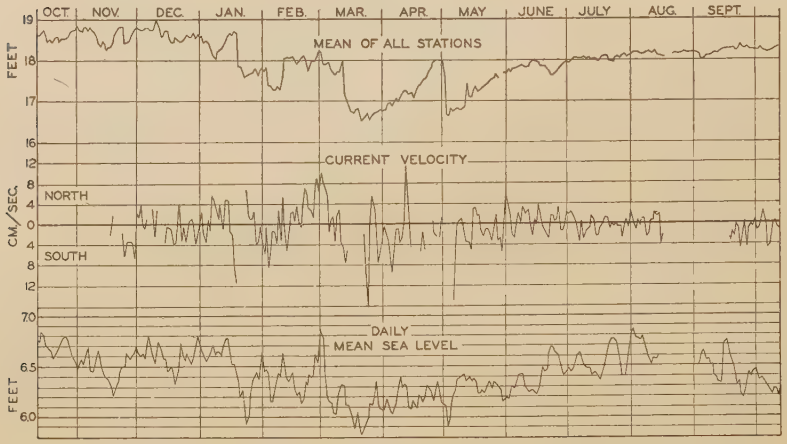


Fig. 5. Comparison of the fluctuations in the mean sand level for all the stations along the pier, with current movements and also with the variations in daily mean sea level.

The Influence of Mean Sea Level.

Mean sea level is obtained by taking the mean of the hourly heights of tide for any desired period. This has been done for each day (Text Fig. 5). The sea level is closely related to the speed and direction of the currents.[4] It will be noted that the three strongest currents to the south approximately correspond in time in the same order with the three lowest sea levels. Also, the second highest velocity to the north occurred the day after the highest sea level of the year.

The daily and weekly sea level curves probably show as close

[4] LaFond, Eugene C.: "Variations of Sea Level on the Pacific Coast of the United States." Sears Foundation: Jour. of Mar. Res., Vol. 2, No. 1, pp. 17-29, 1939.

a correspondence with the changes of mean sand elevation along the pier as with any of the various other factors considered. The sea level even goes through the same annual cycle as the sand, with a depression during the winter and spring and a rise in summer. The changes, however, will be observed to occur in general somewhat ahead of the changes in the sand level. This close correspondence has been observed for several years.[5] The changes in sand level occurring during a change in sea level are mostly due to the currents which primarily control the sea level. However, some variations in sand height must be caused by the differences in water level itself.

Effect of the Wind.

The wind plays an indirect part in fill and cut along the pier since longshore winds influence currents and strong onshore winds in addition produce large waves. The wind records show that the time of lowest stand of sand both on the beach and along the pier corresponds roughly with the period of occasional high wind velocities, in this case from the middle of January till the beginning of May. Wind velocities at La Jolla do not run very high. The maximum recorded wind during this period averaged 26 miles an hour for the 24-hour period. This was accompanied by a large cut along almost the entire pier.

Combination of factors producing large cuts.

Three unusually rapid and striking cuts were general in their effect (Text Fig. 5). In each case within a couple of days the sand level showed an average lowering of over a foot. It has already been shown that the currents reached a maximum to the south on these occasions, and that the sea level showed a correspondingly large lowering. However, other factors combined to produce these results. Thus the large changes about the middle of March and in early May were accompanied respectively by the second largest and the largest waves of the year. The large change in January corresponded only with the fifth largest waves of the year, but the wind velocity at this time reached its maximum for the year. Also the tides in the case of each of these large cuts had just passed the maximum spring range so that they were having their greatest action on the beach. Thus it can be seen that a combination of various

[5] LaFond, Eugene C.: "Relationship Between Mean Sea Level and Sand Movements." Science, Vol. 88, No. 2274, pp. 112-113, 1938.

influences serves to produce the greatest removal of sand in a near shore area of this type.

Underlying Causes of Cut and Fill.

Having shown what factors produce cut and fill it remains to discuss briefly the reasons why these agents act as they do. This is not an easy undertaking, particularly as regards the influences of currents and sea level changes. Accordingly, the suggestions should be considered as tentative and probably subject to change as the work continues.

Waves approaching the coast stir up the sediment on the bottom thus developing a suspended load. The stirring effect is, of course, particularly important in the breaker zone. The motion of the water is more violent towards the shore, however, as it moves seaward more slowly and for a longer period of time.[6] As a result coarser particles tend to move towards shore whereas finer particles move seaward. Probably this same influence is developed where the water thrown towards the shore by waves is returned as a rip current.[7] The latter carries fine sediment outward but has less effect on the coarse sediment. During large wave periods the greater turbulence causes the landward movement to be confined to particularly coarse material such as gravel, if any is available, while the outward moving rip currents find plenty of sand available for transport seaward. With small enough waves, on the other hand, only the forward surge is powerful enough to move the sand typical of this region. Therefore, the sand is carried toward the beach.

Currents and sea level have been shown to follow very similar trends and that, so far as effect is concerned, the currents are the important factor. When the currents are moving to the north they are probably damped by the pier, so that deposition tends to form on the south side which is the side on which soundings are taken. However, taking soundings on the north side of the pier has shown that this explanation is only a partial solution. Possibly the change of the current to the north from its usual southerly direction causes the normal southerly shift of sand along the coast to be interrupted, causing deposition.

The effect of tidal range is partially explicable on the ground

[6] Interim report, Beach erosion board, U. S. Army Engineers, April 15, 3/33-3/35, 1933.

[7] Shepard, F. P.: "Undertow, Rip tides and Rip currents," Science, Vol. 64, pp. 181-182, 1936. Shepard, F. P., and LaFond, E. C.: "Undertow," Science, Vol. 89. No. 2300, pp. 78-79, 1939.

that the high tides of the spring tide periods allow waves to break nearer shore, and thus stir up sand into suspension in an area where sand is normally not disturbed. Sand having been brought into suspension is likely to be carried away from the area where the waves are acting. Also, the large range of sea level allows stirring of sediment by breakers over a wider belt, with corresponding lifting of more sediment into the water for the currents to carry away.

SUMMARY.

It has been shown that the sand is constantly shifting in level along the Scripps Institution pier. During the stormy season of winter and early spring the sand is shifted from the beach towards the outside of the pier, while it is shifted landward during the calmer weather of summer and early fall. Cutting of sand is produced on the foreshore and in the breaker zone especially by large waves and by waves of long period. Small waves and short period waves produce fill in the same zones. The neap tides produce fill a few feet above mean sea level and spring tides produce cut at the same level. Along the beach the correspondence of large waves with a period of spring tides causes a particularly large cut. North flowing currents, which accompany high sea level, produce fill at least on the south side of the pier, whereas south flowing currents which accompany low sea level produce cut along the pier.

As work continues it is hoped that a more perfect understanding of other factors will be obtained. While measurements to date appear to indicate a recurrent cycle without permanent change, the maintaining of the records for a number of years may show a significant trend. Also, the effect along the pier of changing supplies of sand introduced by winter floods can perhaps be evaluated after more data are available.

University of Illinois, Urbana, Ill.
Scripps Institution of Oceanography,
La Jolla, California.

Contribution No. 84

Reprinted from SCIENCE, March 22, 1940, Vol. 91, No. 2360, pages 273–282.

HE CURRENTS OF THE PACIFIC OCEAN AND THEIR BEARING ON THE CLIMATES OF THE COASTS[1]

By Dr. H. U. SVERDRUP

SCRIPPS INSTITUTION OF OCEANOGRAPHY, UNIVERSITY OF CALIFORNIA

FEEL greatly honored by addressing you here on island which was made and made beautifully by , the shores of which are washed by the waters of Pacific Ocean, and which now during this great sition offers a marvelous display of arts, crafts industries from the many countries around that ocean.

stand here, however, with mixed feelings, partly use my personal experiences of the Pacific Ocean limited and of recent years, and partly because I ys feel that it is a shame to reduce winds and es, the ever shifting sky of the sea, and the vast nse of the ocean to a series of graphs in black white such as those which I shall use to illustrate of my address to-day. However, I can not bring ou the fogs of the Bering Sea, the blue waves of the e-wind belts or the icebergs of the Antarctic. I to present my subject in a cut-and-dried fashion, I feel confident that you will not leave with the ression that the Pacific Ocean is as undisturbed and ves in so law-abiding a fashion as appears from graphs. You are familiar with the sea and know it is ever-changing and tantalizing to those who o understand its moods, but to-night I must gen- ze and simplify.

y address will fall into two distinct different parts. he first place, I wish to give a review of the cur- s of the Pacific Ocean and, in the second place, I to consider the influence which these currents ex- e on the climates of the borderlands of the Pacific n. The reasons for this division of the subject will nore clear when the factors which control the ate of any given region have been briefly discussed. nder climate one understands, as you know, the age weather conditions during a long period of s, as expressed by means of average temperatures nonths and seasons, maximum and minimum tem- tures, amount of precipitation and distribution of ipitation, amount of cloudiness and sunshine, aver- and maximum winds and still other characteristics. sh, however, to add that observations which in y localities have now extended over more than a ary indicate that the climate of an area is not tant but is subject to variations the nature of which we know little about. In order to obtain a basis for comparison meteorologists have agreed that the climate of a region shall be defined by means of observations over a period of thirty years. Successive thirty-year periods will then show if changes take place and, before concluding to-night, I shall find opportunity to draw your attention to the fact that in certain regions conspicuous changes have occurred during the past few decades, changes which though probably not caused by ocean currents are related to them.

The climate of any region depends upon a number of factors, the most important being the latitude upon which is based the division in the three major climatic regions—the tropical, temperate and polar climatic zones. The climate is also closely related to the distribution of land and sea and to the character of the atmospheric circulation. The two most extreme types which are related to the distribution of land and sea are those which are known as continental and maritime climates. The continental type which is found over great inland areas is characterized by warm summers and cold winters and, therefore, by a wide range in temperature between summer and winter, and by warm days and cool nights and thus a wide range between day and night. Mostly, it is also characterized by little cloudiness and little precipitation. In contrast, the maritime climate which prevails over the oceans is characterized by a small annual variation in temperature, cool summers and mild winters, by a very small range of the temperature between day and night, and often by great cloudiness and considerable precipitation. In middle latitudes the general circulation of the atmosphere is directed from west to east, and east coasts are, therefore, greatly under the influence of winds blowing from a large continent, whereas west coasts are under the influence of onshore winds from the sea. In these latitudes the climate of the east coasts of the continents differs, therefore, characteristically from that of the west coasts, the east coasts having a more continental climate and the west coasts a more maritime climate. In equatorial regions the circulation is from east to west and the climatic conditions of the coasts are therefore reversed.

The great difference between the continental and the maritime climates is mainly due to the fact that the solid earth, in contrast to the ocean, does not store any appreciable amount of heat. Only the very sur-

[1] ddress given at the Pacific Science Congress, July 939. Contributions from the Scripps Institution of nography, New Series, No. 84.

face is subjected to temperature changes and the surface temperature is, therefore, greatly raised in summer when heat is received from the sun, and greatly reduced in winter when excessive loss of heat by radiation takes place. Similarly, the temperature is increased during the day and reduced during the night. The ocean on the other hand can store large amounts of heat because in summer processes of vertical mixing distribute the heat absorbed from the sun over a relatively thick layer of water, the temperature of which will be only moderately increased. In winter the loss of heat similarly takes place from a considerable layer of water, for which reason the temperature decrease of the surface of the sea will be small. Even if no horizontal ocean currents existed there would be a marked difference between the climate of the land and that of the oceans, and a difference between the climate of the coast and that of the inland areas. The climate over the oceans would be much more uniform than that over the continents and the climate of the coasts would be milder than that over the inland. Even in such circumstances one could speak about the influence of the ocean on the climate of the coast. I do not, however, propose to discuss this general influence any further, because when dealing with actual conditions it must be taken into account that ocean currents exist which also tend to modify the distribution of temperature of the surface waters and to bring into one area waters which are abnormally warm and into another area waters which are abnormally cold. Thus, the circulation of the ocean will alter the climate over the sea itself and will modify the climate of the coasts, because the current flowing along one coast may be abnormally warm and the current flowing along another coast may be abnormally cold. The influence will evidently depend upon the character of the currents which, again, is controlled by the processes of heating and cooling to which the waters of these currents have been subjected in course of time. It is these particular modifications of the climates of the coasts which I propose to discuss, but before doing so it is necessary, as already stated, first to give a review of the character of the currents and especially to consider the distribution of sea-surface temperature which is related to these currents.

I have already mentioned that the climates of the coasts depend upon the prevailing winds. The same is true when dealing with the climates over the oceans and there the effect is intensified, because the currents in the upper layers of the ocean also depend on the wind, the waters being to a great extent set in motion by the wind blowing over the sea. For two reasons one can not expect, however, to find a perfect agreement between the direction of the prevailing winds and the direction of the prevailing currents. In the first place, the boundaries of the oceans place certain limits upon the motion of the water. If the wind blo permanently against a coast the water can not be c ried against the coast but must deviate to the right to the left and instead of a flow towards the coas current along the latter will develop. I shall be a to show several examples of this process when deal with the actual currents of the Pacific. In the secc place it must be taken into account that the mot of the sea is also governed by certain laws, for wh reason some ocean currents may be expected to devi from the wind system. I shall find opportunity show examples of such currents as well.

Let us first consider the prevailing winds over Pacific Ocean in summer, as related to the distribut of atmospheric pressure (Fig. 1).[2] In this season find one high-pressure area located over the east part of the North Pacific, and another over the east part of the South Pacific, separated by a broad b of low-pressure extending clear across the Pac Ocean somewhat north of the Equator. The hig pressure area of the North Pacific dominates co pletely the wind system over that part of the ocea Near the American coast strong northerly or nor westerly winds prevail but, advancing south, the wir turn through northeast to east-northeast blowing the steady trade winds between the latitudes 10° and 25° N. The persistent northerly winds along t west coast of North America and the steady tra winds represent the most conspicuous features of t picture. Over the western and northern part of t Pacific the winds are more variable and blow the mainly from the south, and in the northern part fr the southwest. It should be emphasized that this p ture represents only the average conditions and th except in the trade-wind belt numerous disturban occur associated with traveling low-pressure areas.

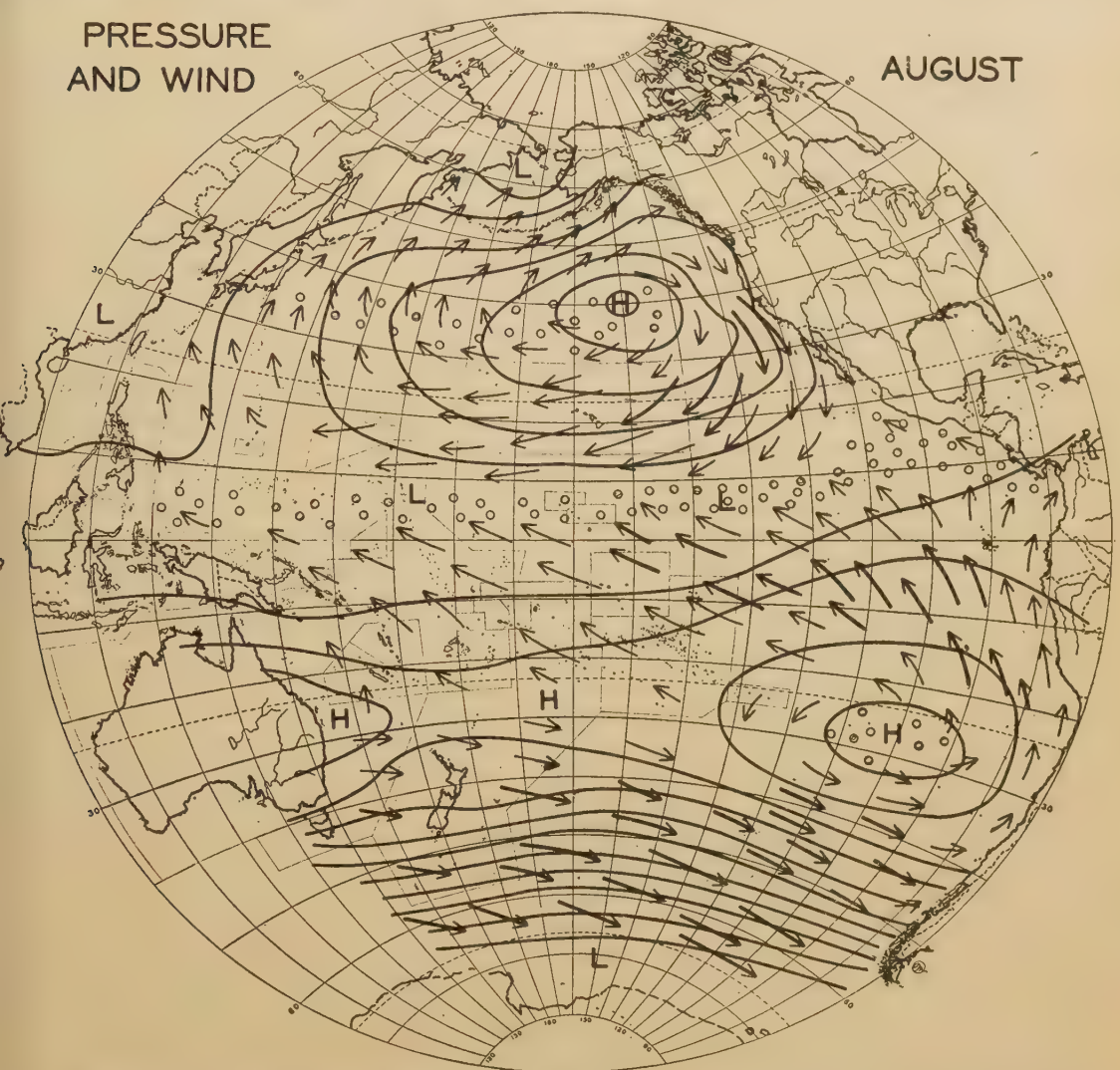
The high-pressure area over the South Pacific sir larly dominates the wind system over that ocea There, the southeast trade winds which blow with hi velocity represent the most conspicuous feature, but the south of the high-pressure area, strong weste winds prevail between latitude 40° S and nearly to t Antarctic Continent. The southerly winds along t west coast of South America correspond to the nor erly winds off the coast of California.

The surface currents in summer (Fig. 2) show close relation to these prevailing winds, but it is i mediately observed that in the northern hemisphe the prevailing current deviates to the right of t direction of the wind, whereas in the southern her sphere it deviates to the left. Within the belt of t northeast trade winds the north equatorial curre

[2] This and the following charts are based on the cha published by G. Schott in his book: "Geographie Indischen und Stillen Ozeans," Hamburg, 1935. Ma 1–4 are reprinted from Robert B. Hall's "Series Maps" published by John Wiley and Sons, Inc.

due west, and, similarly, within the belt of the neast trade winds in the South Pacific the south torial current also flows due west. Along the s the currents must, naturally, follow the coast , but even there a tendency to deviate from the is seen, corresponding to a deviation from the direction to the right or to the left. This deviation of the current from the direction of the wind is flow to the south along the Island of Mindanao, the southern of the Philippine Islands, represents another branch of the same current. This current, which flows against the wind, represents a good example of the effect of the boundaries.

An even more striking exception from the agreement between wind and current is found. Between the two equatorial currents towards the west is im-



. 1. Distribution of atmospheric pressure and prevailing winds over the Pacific Ocean in August (after Schott).

ed by the rotation of the earth but need not be ner discussed here. The main point in this conon is that a general agreement between prevailing s and currents exists. Attention is drawn, how- to the fact that the intensity of the Kuro Shiwo, urrent flowing north along the southern coasts of n, is much greater than should be expected when dering only the weak and variable southerly s. This current must, therefore, be regarded as ntinuation of the north equatorial current. The bedded a swift counter current running towards the east clear across the Pacific Ocean. The counter current is partly met with in the region of calms between the two trade wind systems, but in several instances the current runs directly against the prevailing wind. It has been found that this counter current is very shallow and that the development is probably closely associated with the entire dynamics of the flow, but here it is not necessary to enter upon these matters because the counter current has only a limited influence

on the climates of the adjacent coasts. The counter current serves, however, to bring out the facts that the ocean currents depend not only upon the wind, but that the types of flow which can exist in the sea must also be considered, and that the relation between wind and current is more complicated than would appear from the brief presentation which is given here. It should also again be emphasized that the picture is greatly simplified and that superimposed on the aver-

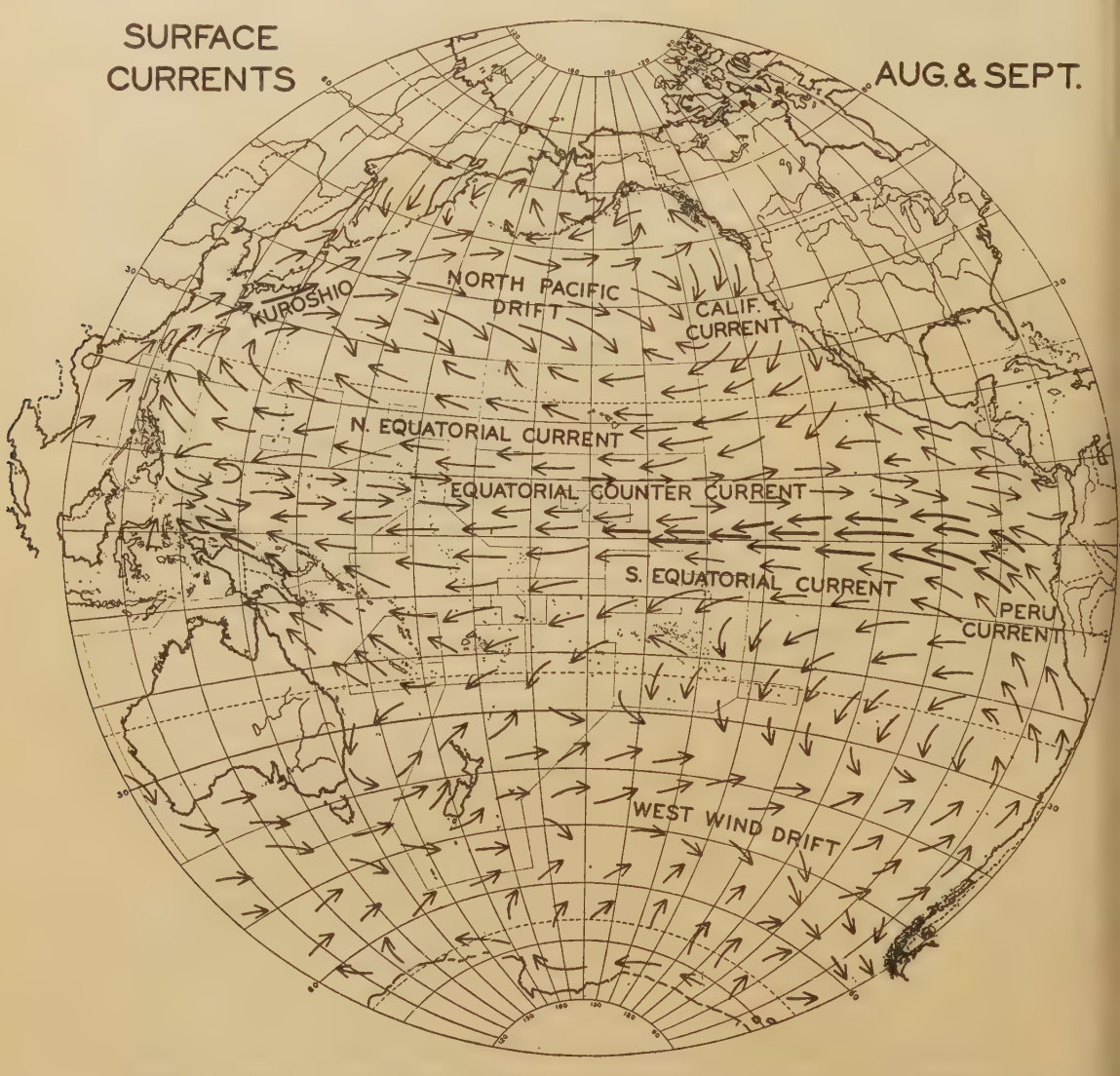


FIG. 2. Surface currents of the Pacific Ocean in August and September (after Schott).

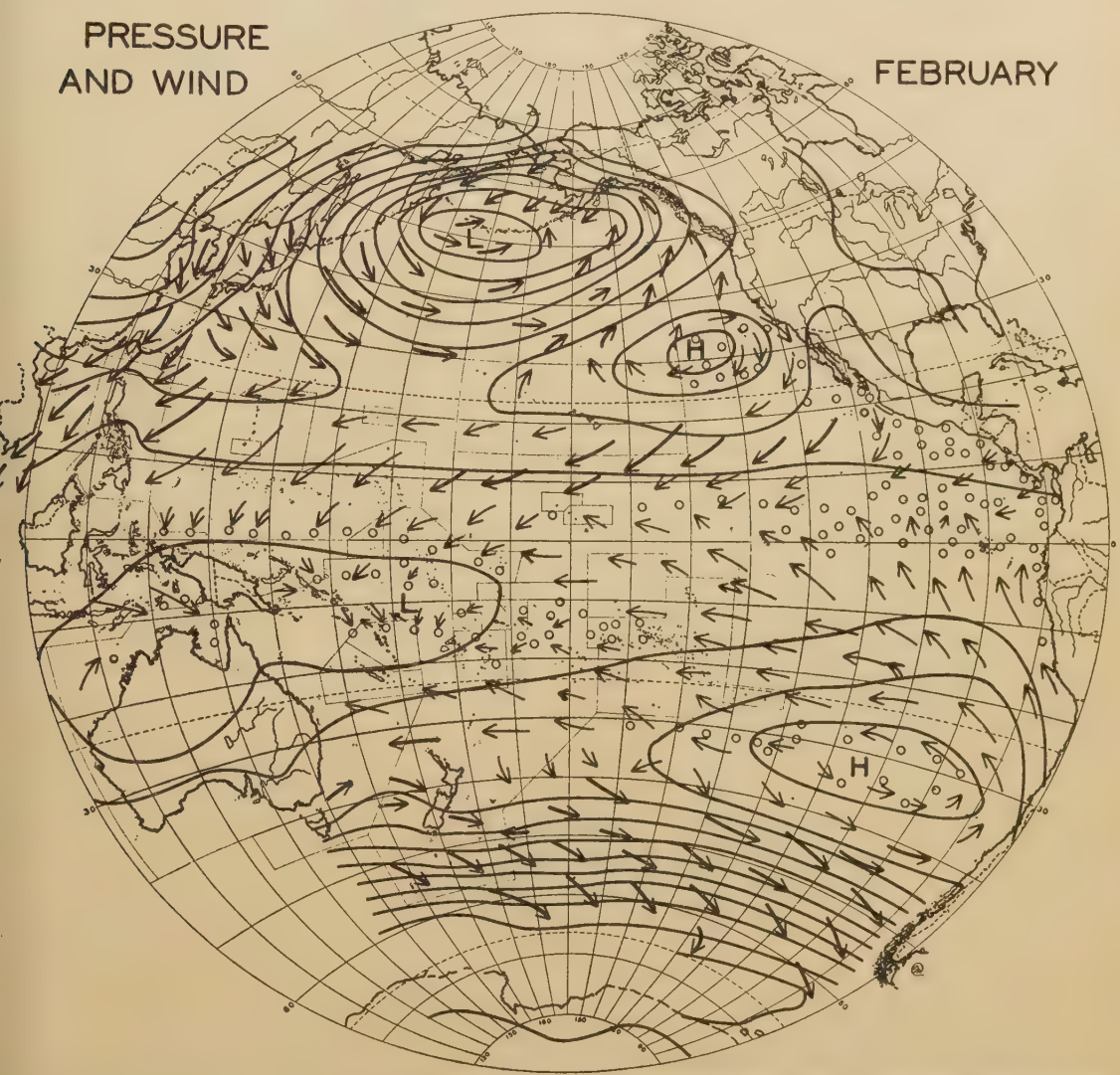
age flow are numerous swirls and eddies and the currents are changing and shifting as are the winds.

In winter much greater discrepancies are encountered between the prevailing winds and currents. The high-pressure area of the North Pacific Ocean is in winter found further south and closer to the American coast (Fig. 3). This high-pressure area no longer completely dominates the circulation, as was the case

in summer, but the more conspicuous feature is no presented by the low-pressure area in the region the Aleutian Islands and by a tongue of high-pressu extending from the Asiatic continent. Along the we coast of America the prevailing northerly winds ha been replaced by weak and variable winds, althou the direction from the north is still the most freque The northeast trade winds are still very conspicuo and have increased in velocity because a steep barometric gradient has been created by the approa of the high-pressure area towards the Equator. Th blow with great permanency over a large area of t ocean between latitudes 5° N and 20° N. The m conspicuous contrast between winter and summer found in the western part of the Pacific, where t weak southerly winds of the summer have been placed by strong northerly or northeasterly wi

ing from the Siberian high-pressure area, and in northern part of the ocean, where strong westerly s prevail.

ne high-pressure area over the South Pacific Ocean ll the conspicuous feature over that portion of the but it has moved away from the Equator. The metric gradient has decreased, for which reason southeast trade winds have decreased greatly in and the current is now found in the western part of the North Pacific, where the north equatorial current bends to the north and continues along the coast of Japan as the Kuro Shiwo, flowing nearly directly against the strong winds from the north. Along the coast of California the current still flows south at some distance from the coast, but an inshore current flowing north has developed. In the southern hemisphere the



3. Distribution of atmospheric pressure and prevailing winds over the Pacific Ocean in February (after Schott).

gth. The intensity of the westerlies in the south-part of the ocean has also decreased.

e surface currents do not show such conspicuous ges as the wind system does (Fig. 4). The north south equatorial currents are still well developed particularly the north equatorial current is more icuous than in summer. The counter current is present but appears to be much narrower. A icuous discrepancy between the prevailing winds south equatorial current has decreased in intensity, but on the whole the picture has remained unaltered.

The turn towards the north of the north equatorial current and the continued existence of the Kuro Shiwo presents an excellent example of the effect of the boundary of the oceans upon the development of the currents. The flow of the north equatorial current towards the west is maintained by the permanent trade winds, and the North Pacific drift from the west to east in

higher latitudes is intensified by the strong westerly winds. Water is therefore transported towards the coast of the Philippines and must bend north along the coast of Japan, or south along the Philippine Island of Mindanao, where the current is strengthened, probably owing to the northerly winds. The greater

tudes, whereas along the eastern boundaries water fr high latitudes is transported towards the equator regions. These transports of water are directly flected in the distribution of surface temperatures. the North Pacific Ocean water of a temperature 70° (F.) is in August found off the coast of Jap

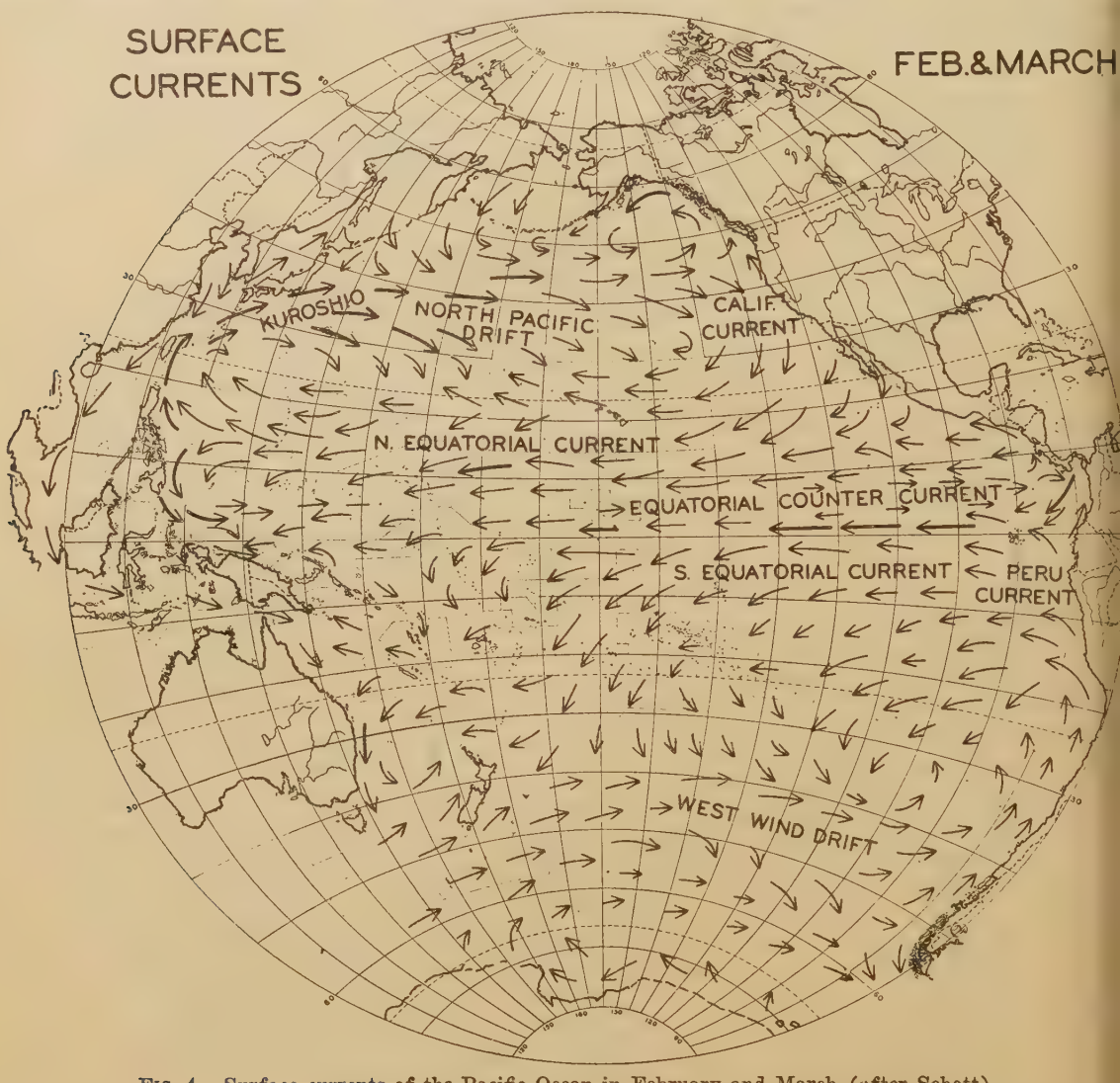


Fig. 4. Surface currents of the Pacific Ocean in February and March (after Schott).

development of the cold Oya Shiwo north of Japan may also be greatly due to the stronger winds from the north.

The inshore flow along the coast of California is an interesting example of a counter current which probably can not be explained as the result of wind action but appears to represent a link which is dynamically conditioned, as is the case with the equatorial counter current.

The main feature of the Pacific surface currents is thus that along the western boundaries of the ocean equatorial water is transported towards higher lati-

in latitude 40° N, whereas off the American coast wa of that temperature is met with in latitude 25°. bend to the north of the isotherms in the western p of the ocean and to the south in the eastern part closely associated with the movement of the wa masses, the warm water of the Kuro Shiwo trav from the equatorial regions towards the north, wher the cold water of the California currents flows fr higher latitudes towards the south. In the Gulf Alaska the flow is, however, from the south, and th relatively warm water is found.

Along the west coast of the United States the ef

ne flow from the north is accentuated by the up-
ng near the coast. North of San Francisco, in
ude 40° N, the average surface temperature of
water near the coast is on occasions as low as 50°,
reas in the same latitude off Japan the temperature
)° or higher. The very low temperatures are due
pwelling, which is a direct effect of the prevailing
ls blowing parallel to the coast. Owing to the rota-
of the earth the surface current tends to be
cted to the right of the wind and, as a consequence,
ight and warm surfaces of the waters are carried
y from the coast and must be replaced by water
n some greater depth. An overturning takes place
because the deeper water has a lower temperature
water becomes accumulated along the coast. I
particularly to point out that the upwelling water
not come from any great depth. The overturn
s place within the upper 500–600 feet and it is
efore essentially a process which takes place within
surface current. The upwelled water does not rep-
nt Arctic or Antarctic deep water as is occasionally
ed.

n the southern hemisphere a similar process of
elling acts along the coast of Peru where water of
nperature as low as 62° is found in latitude 2° S.,
reas in the corresponding latitude on the coast of
Guinea the surface temperature is about 83°. A
ue of low temperature extends along the equator
is associated not only with the upwelling along the
t of Peru, but also probably with a divergence of
south equatorial current tending to raise the sub-
ace waters.

n the winter the effect of currents on the distribu-
of surface temperatures is much less conspicuous
ne North Pacific than it is in summer. In middle
udes there still exists a somewhat similar contrast
veen the coasts on the western side and the eastern
of the North Pacific. In somewhat higher lati-
s the effect of the currents is more conspicuous.
vinter the cold Oya Shiwo brings water of very
temperature to the northern coasts of Japan,
reas the North Pacific drift brings waters of rela-
y high temperature to the Gulf of Alaska. In the
hern hemisphere the upwelling along the coast of
n is as conspicuous as in winter and the tongue
)w temperature along the Equator is still present.
eaving the question of the ocean currents and turn-
to the climate I shall have to limit my discussion
consideration of the temperature conditions. A
t of the air temperature over the Pacific and the
cent coasts in summer shows that over the ocean
air temperature is very nearly the same as that of
surface waters. The isotherms show the same
ls, and in the North Pacific the northward trend
he isotherms along the coast of Japan and the
southward bend along the American coast are particularly conspicuous. Similarly, in the southern hemisphere the effect of the cold current along the coast of Peru is clearly visible.

From the course of the isotherms it is evident that the effect of the currents is limited to a very narrow coastal strip. This is particularly seen when examining the air temperature on the west coast of North America and the west coast of South America. Close to the coast the isotherms bend towards the Equator, but over the land they turn sharply away from the Equator. An air temperature of 70° is thus, on the coast, found as far south as off Lower California but, inland, north of the latitude of Vancouver. In the southern hemisphere a temperature of 70° is, on the coast, found nearly at the Equator, but inland south of latitude 30°. Along the coast of Japan the surface temperature of the sea also tends to reduce slightly the air temperature on the coast, but there the effect is very small as evident from the small bends of the isotherms. Thus it appears that in summer the influence of ocean currents is particularly conspicuous along the west coasts of the American Continents, but of small importance along the east coast of the Asiatic Continent.

In February the influence of the ocean current is in the northern hemisphere much less striking, except that in the Gulf of Alaska the coast has a much higher temperature than the inland, owing to the relatively warm water which flows through the Gulf of Alaska. Further south along the west coast of America the influence of the sea decreases. In the Japan region and along the east coast of the Asiatic Continent the air temperature is in winter much lower than the temperature of the adjacent sea, and there the cold air which flows out from the Siberian high-pressure area exerts a greater influence than do the ocean currents, but the latter tend to modify the winter cooling. Conditions in the southern hemisphere are, in February, naturally related to those which existed in the northern hemisphere in August.

The general features which have been discussed so far can also be brought out better by considering specific examples of difference in the annual march of temperature on both sides of the Pacific Ocean. Yokohama and Berkeley are nearly in the same latitude but the annual march of temperature in these localities is widely different, as evident from Fig. 5, in which are shown the mean monthly temperatures. At Yokohama the average temperature of the coldest month is as low as 37° but the warmest month has an average temperature of nearly 80°. The great range of 43° clearly demonstrates the continental character of the climate of Yokohama. In Berkeley on the other hand the coldest month has an average temperature of 48° and the warmest is 62°, and the small range of

only 14° clearly demonstrates that Berkeley, from this point of view, has a maritime climate.

A comparison of the air temperature with the water temperatures off the coasts is of further interest. Off Yokohama the water temperature varies during the

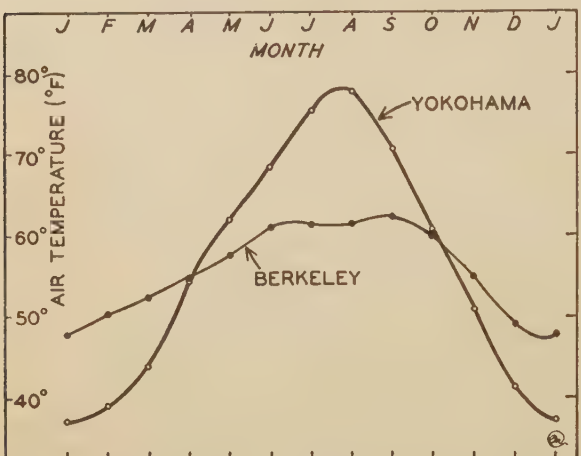


FIG. 5. Mean monthly air temperatures at Yokohama and at Berkeley.

year between 62° and 80°, and in nearly all months the water is warmer than the air. The great difference in winter is particularly striking and is due to the fact that the northerly winds bring air of low temperature. At Berkeley on the other hand the water temperature off the coast varies only between 52° and 58°. The coldest water is found in April and May because in these months the upwelling which was previously mentioned is most intense. The air temperature remains throughout the year very close to the water temperature but is generally somewhat higher. It is quite evident that the low spring temperatures at Berkeley are closely associated with the cold waters off the coast, and that at Berkeley the air temperature is to a great extent controlled by the temperature of the currents off the coast in contrast to the conditions at Yokohama. At Yokohama the warm water off the coast makes the winter milder, but the air temperature is not completely controlled by the water temperature. The difference is due to the fact that in Yokohama offshore winds prevail during the winter, whereas in Berkeley onshore winds prevail. The specific influence of the ocean currents gives Berkeley an abnormally low summer temperature and a relatively high winter temperature.

The annual march of precipitation in the two localities also shows a conspicuous difference. At Yokohama the precipitation is considerable in all months of the year, the mean monthly values varying between about 2.5 inches in winter up to 10.6 inches in the early fall. The excessive rains in the month of August, September, October are in part attributed to the influence of the adjacent sea because the path followed by the are of low pressure will, to a considerable extent, be co trolled by the temperature distribution over the ocea The currents off the coast are therefore of considera importance to the climate of Yokohama, although t continental character prevails as far as the tempe ture is concerned. At Berkeley on the other hand precipitation falls in midsummer, but the wint months have up to 4 or 5 inches. The lack of precip tation in summer can in this case be ascribed partly the effect of the inland and, as far as precipitation go Berkeley is more continental in character, although t temperature curve is distinctly maritime in type. Th the bearing of the currents on the climate is a co plicated one and it is here possible only to draw atte tion to some of the more outstanding features, and pay particular attention to the distribution of te perature.

Turning to the southern hemisphere it is again interest to compare conditions in the east and in t west, and for this purpose Fig. 6 shows the air a

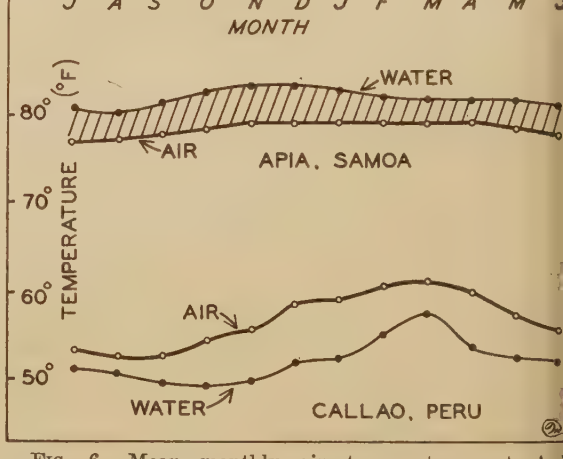


FIG. 6. Mean monthly air temperatures at Api Samoa, and at Callao, Peru, and mean monthly sea surfa temperatures off the coasts.

water temperatures at Callao, Peru, and Apia, Samo which are located in 12° S and 14° S., respectivel The curves have been plotted with the month of Jan ary in the center, because January is a summer mon in the southern hemisphere.

At Apia, Samoa, the annual range of the air te perature is very small and the air temperature alwa remains somewhat lower than the temperature of t water, which is about 80° throughout the year. Callao, Peru, the air temperature is much lower tha it is at Apia and varies between 52° in winter and 6 in late summer. The air temperature is througho the year higher than the temperature of the waters the coast which varies between 49° and 57°. It c not be doubted that both at Apia and at Callao the a

peratures are completely controlled by the temtures of the water. At Callao the low water temtures are the results of the character of the ents off the coast which carry cold water from er latitudes towards the Equator and within which surface temperature is further reduced by upwell-

The lowest water temperatures occur in the ths of October, which in the northern hemisphere esponds to April, the month of the lowest water peratures off the coast of California.

he most striking conclusion which can be based on very brief review is that a direct influence of the n currents upon the climates of the coasts is pararly found on the eastern side of the Pacific Ocean, reas the coasts on the west side are only slightly enced by the currents. On the eastern side of the fic the cool summers on the coast of South America on the coast of North America between Cape San as at the southern end of Lower California and rds the strait of Juan de Fuca are directly related he character of the currents. Similarly, the mild ers of the coast of British Columbia and Alaska directly related to the relatively warm currents h bend north into the Gulf of Alaska. The direct ence of the sea is, however, limited to a very narcoastal zone, as you all know from personal rience.

hen discussing the influence of oceans on climate, ffect of the northern branch of the Atlantic Drift, he Gulf Stream, upon the climate of northwestern ope is very often considered the most magnificent nple of such influence. In this case the influence ot limited to a narrow coastal strip because the e character of the atmospheric circulation appears e modified by the surface temperatures of the n. The high temperature of the Atlantic water h enters the North Sea north of Scotland causes atmospheric lows to take a more northerly path thus to bring warm maritime air in over large ions of northwestern Europe. The areas which come under the influence of ocean currents are greater than the coastal areas of the Pacific, but tention is paid only to the very coasts the modifins of the climate which may be ascribed to cur- are as great along the coast of the Pacific Ocean ywhere else in the world.

conclusion, it may be of interest to examine the ion whether changes of climate can be attributed anges of ocean currents. It has then in the first to be observed that the development of ocean nts depends to a great extent upon the boundaries he ocean and the depth to the bottom. Major ges of the bottom configuration or the coast lines lead to major changes in the flow of the water and to appreciable alterations of the climate. Scotand Iceland are connected by a submarine ridge. If this ridge should rise, the volume of Atlantic water flowing into the North Sea would be reduced, and if the passage should become completely closed the effect upon the climate of the Scandinavian countries would be disastrous, and these countries would perhaps face a new glacial period. On the other hand, if the Aleutian Islands should sink into the sea and Bering Strait should widen and deepen, the Pacific west wind drift might turn north; Alaska would probably receive a much milder climate than what it has now, and the Yukon Valley might become covered with orchards. Such changes may take place during long geological periods, and it is possible that changes of this nature have had bearing on the past climates of the Pacific area and may receive bearing on the climates of a very distant future, but in a discussion of climatic changes in geological periods many other factors enter in, particularly changes in solar radiation.

It is of more immediate interest to examine the question whether variations of short duration in the character of the currents occur, and, if so, whether these variations will be reflected in similar changes of the climates of the coasts. This question is a very complex one because the ocean currents are determined to such an extent by the prevailing winds that any change in the general circulation of the atmosphere will lead to a change in the ocean currents, but such a change in the general circulation will also have direct bearing upon the climate of any particular region. It is therefore difficult to discriminate between the direct influence upon the climate of a change in the atmospheric circulation and the indirect influence which is brought about by an alteration of the ocean currents. We have a striking example of this condition in northwestern Europe. During the last thirty years the winters of northwestern Europe have become milder, and the most conspicuous change has taken place in northern Norway and in Spitsbergen. In Spitsbergen the average winter temperature has, during the last decade, been about 15° above the average winter temperature of forty years ago. There is good evidence that this rise of winter temperature has been accompanied by a greater transport of Atlantic water towards the north. The increase in the volume of warm water flowing along the coast has certainly a bearing on the climate but the greater part of the change may not have been directly caused by such greater transport. Both the major effect on the climate of Spitsbergen and the effect on the currents of the North Atlantic Ocean may be due to a displacement towards the north of the tracks of the low-pressure areas. Such a change of the atmospheric circulation may again be due to a slight alteration of the amount of energy received from the sun which keeps the atmosphere running and maintains the ocean currents.

It should be borne in mind that the atmosphere and the ocean represent two delicate thermodynamic machines which are interdependent. A change in the performance of one of them leads to a change in the other which brings about a new reaction in the first one. A balance—a steady state is never attained. In order to understand the complex sequence of events and to be able to discriminate between changes in climate caused directly by changes in atmospheric circulation and indirectly by changes in ocean currents, it is necessary to acquire a better knowledge of both the atmosphere and the ocean and of the interaction between the two. At the present time it is possible only to state empirically how the climates of the coasts are influenced by the ocean currents. If we wish to comprehend the mechanism of this influe and to predict what changes we may expect as circulation of the atmosphere is subjected to chan we have to know how the enormous machines rep sented by the atmosphere and the ocean really wo When dealing with the atmosphere great advances h been made in recent years, largely because it has b possible to secure and to interpret upper-air obser tions, but when dealing with the oceans progress slow because of the difficulties of obtaining adequ data. This, however, should not discourage us should be an added reason for increasing the efforts the study of the currents of the oceans and parti larly of the Pacific Ocean which, at the present ti is less known than any other ocean in the world.

Contribution No. 86

Reprinted from Turtox News, Vol. 18, No. 4, April, 1940.

LIFE IN A DROP OF SEA WATER

by
W. E. Allen
Scripps Institution of Oceanography
University of California
La Jolla, California

Contributions from the Scripps Institution of Oceanography, New Series, No. 86

Of course, there is actually no such thing as a drop of sea water. Imagine a sea composed of spherical units near the size of a dry seed of "sweet pea." As a matter of fact, the sea is a mass of confluent liquid with no visible trace of divisibility into any kind of units. Furthermore, a drop removed from this confluent mass is sea water no longer. It is merely a drop of salt water which more or less nearly resembles the sea water from which it was taken, according to the conditions of taking, the lapse of time since the taking, and the conditions of exposure after the taking. Nevertheless, it is convenient, sometimes, to pretend that there are drops of sea water and the fiction involved is no greater than that often used in all kinds of sciences, even the "exact sciences."

Therefore, let us pretend that we can find drops of sea water which may be treated as microcosms. However, it must be kept in mind that one drop of sea water may differ extremely from another in composition and in inclusions. For example, one drop may contain only the faintest trace of oxygen, even as a constituent of some included compound, although another may contain much oxygen in solution, in combination and in mixtures. The first drop would be unfavorable for life while the other might be highly favorable. An indefinite series of possible differences between two drops might be mentioned, not only similar to these as concerns other substances but also dissimilar in respect to some. The essential point is that our fictional drops of sea water can and do differ in chemical, physical, and biological characteristics. For such reasons, if for no others, discussion of possibilities of life in a drop of sea water must be more or less "sketchy."

If one should search for a drop of sea water totally devoid of life he would be more likely to find it in mid-ocean rather than near shore. Indeed, it seems probable that at a distance of a thousand miles from shore and at a depth of one mile he might find many more drops devoid of life than he might find that contained one or more living things, either active or dormant. But, it is also fairly certain that he could not be sure of extracting a barren drop at any particular point in any sea. That is to say, conditions at any point in the sea are never predictable for any particular moment of time.

Notwithstanding the numerous obstacles to precise observation of a drop of sea water, it is possible to offer considerable evidence of certain common conditions and to state plausible inferences about others. Doubtless the first question to occur to most people about life in a drop of sea water would be concerning the kinds of living things most likely to be found in one. A safe reply is that either or both animals and plants may be represented within its limits. Indeed it is possible for a dozen kinds or more to be represented in a single drop, sometimes a mixed population of animals and plants but more often only plants and possibly only animals. However, even in dense populations, the number of different kinds may be expected to be smaller than that. While adjoining drops are likely to be closely similar in this respect it is entirely possible for them to differ notably. Possibly one drop will contain only representatives of a single species while another beside it contains representatives of one or more species. This especially is probable concerning bacteria and their kin although it may be true of many kinds of organisms slightly larger than the bacteria.

There are so many thousands of different kinds of living things (including forms as high as fish eggs and sperm) which might be found represented in a drop of sea water that we must select for notice only a few of the more prominent groups. Admitting (on the basis of probability) that bacteria and their close kin may appear most frequently and in largest numbers it seems fair to say that free living (planktonic) diatoms are most often conspicuous. They are microscopic plants but most of them are larger than most marine bacteria and their large populations attract attention more readily. Also widely distributed and likely to be represented in any drop of sea water are the dinoflagellates, border line organisms some

of which are generally admitted to be plants while others are in dispute as to characteristics. More restricted in range and locality distribution are coccolithophores and silicoflagellates, two groups often represented in sea waters adjoining American shores. Most famous of the many kinds of protozoa which might be represented in a single drop of sea water are the foraminifera, the creatures which are so often used by oil geologists in trying to trace petroleum deposits. Radiolarians are only a little less prominent in many seas. Naupliar stages of plankton copepods are frequently found as far from shore as two hundred miles and even if they occur no more abundantly than one to every thousand drops of water they deserve mention because of their wide distribution. They might not live long in a single drop of water but they are small enough to be easily enclosed in one. Doubtless many other kinds of very young forms in widely different groups should be mentioned also as possible inclusions. This is especially true if a sample drop be taken from sea water near shore; where myriads of sedentary animals and plants shed spawn and spores into the water to compete for space with the kinds which live free swimming or free floating lives. Oysters, mussels, barnacles, worms, and "sea weeds" and hundreds upon hundreds of other kinds of living things all have stages of existence small enough to be accommodated in a drop of sea water, at least temporarily.

Through most of the year space relationships are not oppressive for any inhabitant of a drop of sea water. For example, most diatom cells are so small that two or three hundred could be enclosed in a drop without appearing to be excessively crowded. But such numbers do not occur often in the most favorable localities and never in some unfavorable localities. Through most of the year only a single cell or a single colony of cells is likely to be found. Even then adjoining drops may be vacant. Suppose that a single diatom cell occupies the center of the fictitious drop. Keeping in mind the spherical surface limits of the hypothetical drop it is fairly easy to realize that any particle (in the sense of any subdivision of matter, however small) at any point in that spherical surface may be influenced by the centrally located cell or may exert influence upon that cell. For example, a loosely bonded carbon dioxide molecule may be dissociated from combination at the periphery and attracted to the cell. Per contra a newly released oxygen molecule may be liberated by the cell to find a bond at some point in the periphery. That is to say, within this microcosm influences may pass inward or outward between cell and periphery on any of an infinite number of radii extending from the center of the drop to the infinite number of points in the spherical surface. This condition may seem complicated enough but the actual conditions are far more complicated.

For one thing, no notice has been taken of the influence of gravity upon the cell itself and upon the results of influences such as those just mentioned, influences which would be decidedly different on different radii of the fictional drop. Nor has any notice been taken of the influences of light or other radiant energy which are sure to be deeply involved in reciprocal influences relating to the cell and particles anywhere within the drop. Likewise the exact composition of the drop of water and the details of its inclusions have been ignored although having a direct bearing on the degree and kind of influences exerted reciprocally between the cell and a peripheral particle. No less important in respect to reciprocal relationships of this kind are details of structure and composition and of activity of the cell. In other words conditions of life in the fictitious drop are not so simple as they may appear to be at first thought.

This inherent complexity becomes still more apparent when one considers the possibilities or probabilities which may result from the addition of one or several other individuals to the microcosm whether of the same kind or of other kinds. If the original, centrally located cell divides into two, complexities are not necessarily doubled or multiplied but they are more intricately entangled. Both cells cannot hold the center of the drop. There is an initiation of a competition for space. How they move apart no one knows, at least for some species, but there is a difference in position, nevertheless, and that alone is likely to modify the influences exerted upon or received from particles on the borders or within the drop. Add a few bacteria and the possibilities of modification of reciprocal relationships become bewildering. Add a dinoflagellate, a foraminiferan, and a nauplius and these possibilities of modification become inextricably confused. But this does not end the catalog of contributions to confusion. The fictitious drop is surrounded on all sides

by an indefinite series of neighboring drops (or equivalent masses). In some or all of them reside sources of influence while through any or all of them more remote influences are being transmitted. Surely a discouraging prospect for any investigator. But not more so, really, than any life prospect elsewhere.

I have heard of biologists whose discussions of problems of life consist largely of juggling of such terms as "limiting factor," "dominant factor," "optimum," "minimum," "maximum," and the like. Like most, if not all, of us they desire to fix things so that they will stay fixed, to settle questions so that they will stay settled, and to solve problems so that they will stay solved. The magic of positive use of definite terms helps them to feel that they are successful. However, no one has ever yet succeeded in placing shackles on life in Nature, not even word shackles. But, as suggested in the opening paragraph, it is convenient sometimes to pretend that things are true and such pretense is permissible if properly used. It should never be allowed to place fiction ahead of fact. At a given moment, oxygen tension in our hypothetical drop of water may be really a "dominant factor" in directing the activities of the hypothetical single cell. In the succeeding moment a deficiency in available nitrogen may be "dominant." Or throughout the life of that particular cell either one of these influences may be "dominant." But if we interest ourselves too strongly in the influence which we call "dominant" we may overlook another which is no less essential because we ignore it. If a man attacked by two thugs, one big and one little, gives all of his time to the big one he may be easily knocked out by the little one whom he neglected.

Fortunately for investigators of life and of the conditions of its existence, life activities, life influences, and environmental influences tend to appear in groups wherein one or more relatively conspicuous items are found to be representative. Thus, in our hypothetical example of relationships a retardation of some activity of the single cell may be explained to our satisfaction by reference to temperature although we know that viscosity, diffusion, chemical activities and a number of other influences are involved. So long as we remember that temperature may be the symbol of a group of influences rather than being strictly a determining influence in itself we need not go far astray by pretending that temperature constitutes a satisfactory reason for changes observed in apparent response to it. It seems safe to say that by judicious use of the more symbolic "factors" or influences we may arrive at a practical understanding of life in a drop of sea water, or anywhere, which is reasonably sound and dependable.

Contribution No. 88

Contributions from the Scripps
Institution of Oceanography
New Series, No. 88

Reprinted from JOURNAL OF BACTERIOLOGY
Vol. 39, No. 3, March, 1940

THE EFFECT OF OXYGEN TENSION ON THE OXYGEN UPTAKE OF LAKE BACTERIA[1]

CLAUDE E. ZOBELL[2] AND JANICE STADLER[3]
University of Wisconsin, Madison

Received for publication July 7, 1939

Many studies have been made on the influence of oxygen tension upon the growth and activity of various organisms (Amberson, 1928, Hyman, 1929), but relatively few measurements of oxygen consumption have been made. Although it is generally agreed that most bacteria have definite oxygen optima for multiplication and for certain physiological activities, no generalizations can be made from the fragmentary literature on the influence of oxygen tension upon the rate at which oxygen is consumed by respiring cells.

Escherichia coli was found by Stephenson and Whetham (1924) to consume much more oxygen in an atmosphere of pure oxygen than in one of air. Wohlfeil (1930) also noted that the rate of oxygen consumption by this organism is proportional to the oxygen tension. Similarly Novy and Soule (1925) found that the maximum oxygen consumption by *Mycobacterium tuberculosis* occurred when it was cultivated in an atmosphere containing 40 to 50 per cent[4] oxygen; growth and oxygen consumption decreasing progressively below this value. According to Georgi and Wilson (1933) the respiration of the Rhizobia increases with

[1] This work was made possible by grants from the Brittingham Trust Fund and the Wisconsin Alumni Research Foundation.

[2] Visiting investigator on sabbatical leave from the Scripps Institution of Oceanography, University of California, LaJolla.

[3] Works Progress Administration.

[4] 20 per cent oxygen is equivalent to a partial oxygen pressure of 152 mm. Hg. When in equilibrium with such an atmosphere at 25°C. freshwater will contain approximately 8.6 p.p.m., 8.6 mgm. per liter or 6.1 ml. per liter of dissolved oxygen.

increasing oxygen tension but Burk (1930a) reports that the respiration of the pea *Rhizobium* is independent of oxygen tension. Working with diluted sewage containing from 0.5 to 26 p.p.m.[4] of dissolved oxygen Heukelekian (1936) noted the maximum utilization of oxygen at 15 p.p.m. oxygen. Conversely Pomeroy (1938) found virtually the same amount of oxygen utilization in sewage mixtures containing from 1.0 to 25 p.p.m. oxygen. Waksman and Carey (1935) report that the oxygen consumption of bacteria in sea water is definitely slower at reduced oxygen tensions.

The interpretation of the foregoing observations is complicated by changes in the number of bacteria during the course of the experiment, and there is no basis for inferring that a change in the rate of multiplication indicates a change in the oxygen intake of individual cells. Indeed, Burk (1930b) found that 4 per cent oxygen gave the maximum multiplication of *Azotobacter* but that 21 per cent oxygen was optimal for its respiration. According to the observations of Pütter (1924) on *Pseudomonas nonliquefaciens* and those of Harvey (1925) on *Photobacterium phosphorescens*, under conditions which avoided any appreciable change in number of respiring cells, the oxygen tension does not influence the oxygen uptake per cell. The luminescence of the photogenic bacteria which depends upon oxygen was not dimmed until the oxygen tension was reduced to less than 0.5 per cent. Shoup (1929) records that dimming occurs only when the oxygen tension is reduced to around 0.25 per cent oxygen or a partial pressure of 2 mm. Hg. Warburg and Kubowitz (1929) found that the respiration of *Micrococcus candicans* was just as rapid at an oxygen tension of 0.001 per cent as in air.

EXPERIMENTS WITH MIXED CULTURES IN LAKE WATER

Being interested primarily in elucidating the factors which influence the depletion of oxygen from natural waters in which bacteria are probably the most important agencies (Birge and Juday, 1911, Kusnetzow, 1935), our first experiments were performed with the mixed microflora in Lake Mendota water. An attempt was made to simulate conditions in nature although it is recog-

nized that various changes accompany the storage of water in the laboratory (ZoBell and Anderson, 1936). Since the water contained only enough respirable organic matter to consume 2 to 5 mgm. of oxygen per liter after prolonged incubation, it was not feasible to determine the minute quantities of oxygen consumed from day to day (0.1 to 0.5 mgm. per liter) using respirometer technique. Therefore the water was stored in 145 ml. glass-stoppered bottles and the oxygen content determined by the Winkler method which was accurate to 0.02 mgm. per liter.

Water was collected from Lake Mendota in chemically clean glass bottles, filtered through cotton to remove particulate matter and thoroughly mixed to insure its uniformity in composition and bacterial content. After warming the water to 25°C. the oxygen tension of portions of it was adjusted by washing with tank nitrogen until siphoned samples were found to contain the desired concentration of dissolved oxygen.

It was established that bubbling nitrogen through the lake water to decrease its oxygen content did not otherwise influence the results. In some experiments all of the water was washed with nitrogen until the oxygen tension was less than 0.5 mgm. per liter. Then, enough oxygen was admitted to different lots of the water to provide for concentrations ranging from 1 to 8 mgm. per liter. Under these conditions the results were comparable to those obtained in water from which only part of the oxygen had been differentially reduced to the desired level by merely washing with nitrogen. Moreover, similar results were obtained when the oxygen tension was adjusted by first depleting the oxygen by boiling the water in the autoclave and then introducing different amounts of oxygen.

The water, containing different concentrations of oxygen, was distributed to numerous glass-stoppered bottles under a nitrogen atmosphere. Duplicate bottles were analyzed immediately for dissolved oxygen and the others were analyzed after one to five days incubation in a water-bath at 25°C. Table 1 summarizes the data from a representative experiment.

In corresponding experiments lake water was incubated in 4-liter bottles. Pairs of such bottles completely filled with water

of the same oxygen tension were connected with glass tubing so that water for analysis siphoned from one bottle was simultaneously replaced by similar water from the second bottle. The water thus drawn from the second bottle was replaced by water from a third bottle placed at a higher level than the other two to provide a positive head. This third bottle was filled each time samples were to be taken with the same kind of water with which the other two bottles were filled after its oxygen tension was adjusted to approximately the level indicated by the previous analysis. This sampling technique provided for a closed system except that the water in the third bottle was exposed to the air while samples were being withdrawn. Duplicate samples were

TABLE 1

Oxygen consumed by multiplying bacteria in Lake Mendota water containing different concentrations of dissolved oxygen

INITIAL OXYGEN	OXYGEN CONSUMED AFTER				
	1 day	2 days	3 days	4 days	5 days
mgm. per liter	*mgm. per liter*	*mgm. per liter*	*mgm. per liter*	*mgm. per liter*	*mgm. per liter*
0.78	0.30	0.47	0.57	0.66	0.71
1.75	0.27	0.46	0.61	0.86	0.96
3.36	0.29	0.38	0.53	0.88	0.85
7.82	0.28	0.44	0.56	0.84	0.93

analyzed for dissolved oxygen, and the number of bacteria determined by plating appropriate dilutions with nutrose agar (Henrici and McCoy, 1938).

The results obtained in the 4-liter bottles compared favorably with those obtained in series of 145 ml. bottles. Table 2 presents the composite data from several experiments and shows the amount of oxygen consumed by bacteria in lake water which contained from 0.66 to 7.99 mgm. of dissolved oxygen per liter at the onset of the experiment.

It will be observed that virtually the same amount of oxygen was consumed during the first day, irrespective of the initial oxygen tension of the water. There is also a marked degree of similarity in the amounts of oxygen consumed from water of varying oxygen tension after longer periods of incubation. These

relationships become more evident when the mean values from all of the experiments are plotted graphically as in figure 1.

TABLE 2

Effect of oxygen tension on the oxygen uptake of lake bacteria

TYPE OF BOTTLE	NUMBER OF EXPERIMENTS	INITIAL OXYGEN		OXYGEN CONSUMED AFTER				
		Range	Average	1 day	2 days	3 days	5 days	10 days
		mgm. per liter	*mgm. per liter*	*mgm. per liter*	*mgm. per liter*	*mgm. per liter*	*mgm. per liter*	*mgm. per liter*
145 ml.....	3	0.66–0.79	0.74	0.41	0.58	0.62	0.70	0.73
4-liter.....	4	0.74–0.94	0.84	0.44	0.58	0.67	0.75	0.81
145 ml.....	4	1.42–2.02	1.69	0.40	0.72	0.87	1.31	1.51
4-liter.....	3	1.68–1.91	1.76	0.43	0.75	0.95	1.24	1.48
145 ml.....	4	3.36–4.57	3.77	0.36	0.60	0.89	1.26	1.66
4-liter.....	4	3.47–4.45	3.88	0.46	0.77	1.03	1.46	2.00
145 ml.....	4	6.92–7.82	7.41	0.47	0.67	0.87	1.69	2.39
4-liter.....	3	7.71–7.99	7.83	0.39	0.74	1.09	1.36	2.03

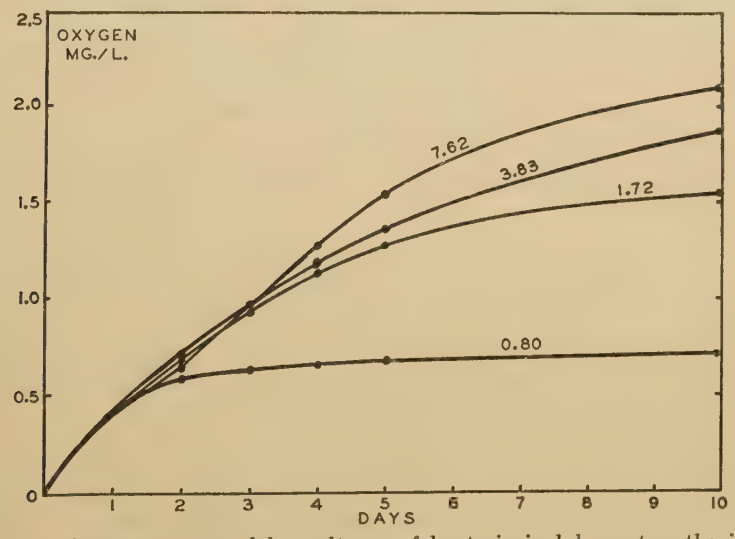


FIG. 1. Oxygen consumed by cultures of bacteria in lake water, the initial oxygen tension of which was 0.80, 1.72, 3.83 and 7.62 mgm. per liter respectively.

Superficially it appears that after one or two days incubation the rate of bacterial respiration is somewhat greater in water containing the higher concentrations of oxygen. However, such a conclusion is not in accord with observed facts. In the first place, as shown by figure 1, oxygen is consumed at virtually the same

rate at all oxygen tensions considered for four or five days, unless nearly all of the oxygen has been depleted earlier. At this time most of the readily utilizable substrate has been oxidized, thereby restricting the rate of subsequent oxygen consumption regardless of the oxygen tension of the water.

Of greater significance in the interpretation of the foregoing results is the changing bacterial population. At the beginning of the experiments the water contained only a few thousand bacteria per milliliter. After one day the number had increased a hundredfold or more, and after two days incubation there were millions of respiring bacteria per milliliter of water. Thereafter the number of bacteria which could be demonstrated by plating procedures decreased sporadically although there were still ten to fifty thousand viable cells per milliliter present after 30 days. After two or three days, the largest bacterial populations were usually found in the water containing the most dissolved oxygen, the higher oxygen tensions presumably favoring the multiplication of aerobes. It is believed that this accounts, at least in part, for the increased oxygen consumption in such water.

In order to estimate the amount of oxygen consumed by each cell per unit of time the formula of Buchanan and Fulmer (1930) was applied:

$$m = \frac{2.303\ \mathrm{S} \log b/\mathrm{B}}{t(b - \mathrm{B})},$$

where m is the amount of oxygen consumed per cell per hour, S the total amount of oxygen consumed in time t, B the number of bacteria at the beginning and b the number after time t. It is doubtful if the formula holds strictly because the bacteria do not continue to increase geometrically throughout the course of the experiment and other requisite conditions do not prevail. However, it is believed that the application of the formula to the data gives an approximation of the amount of oxygen consumed per cell, particularly during the first part of the experiment; and some interesting relationships are revealed by treating the data in this way. Typical results are recorded in table 3.

Although there is no close agreement between the apparent

amount of oxygen consumed per cell per hour in water containing various amounts of oxygen, there are no differences which can be attributed to the effect of oxygen tension. The lack of agreement is attributed primarily to sampling errors since the water in the closed bottles could not be shaken and to the known shortcomings of the plate-count technique for estimating bacterial populations. It is significant that, regardless of the initial oxygen content of the water, there was appreciably more oxygen consumed per cell during the first day than during the second 24-hour interval, and more during the second day than during the

TABLE 3

Apparent amount of oxygen consumed by bacteria during different periods of incubation at 25°C. in lake water containing different concentrations of dissolved oxygen

INITIAL OXYGEN	OXYGEN CONSUMED PER CELL PER HOUR DURING				
	1st day 10^{-12} mgm.	2nd day 10^{-12} mgm.	3rd day 10^{-12} mgm.	4th day 10^{-12} mgm.	5th day 10^{-12} mgm.
mgm. per liter					
0.72	78	5.4	0.21	0.07	0.13
1.68	51	12.8	0.56	2.9	12.0
3.81	69	9.5	0.73	6.0	19.0
7.94	93	24.1	0.40	1.2	4.7

third 24-hour interval. Thereafter the respiratory capacity of the cells appeared to increase.

These anomalous observations can be partly explained. As mentioned above much of the readily respirable organic matter in the lake water is oxidized during the early stages of the experiment. While the bacterial population is increasing more or less geometrically the available organic matter is decreasing, until a lack of the latter after a day or two limits further multiplication while there are still only a few million cells per ml. of water. Consequently there is less and less respirable organic matter for each cell, which accounts for the decreasing respiratory rate. That organic matter is the limiting factor in bacterial multiplication is indicated by the fact that upon the addition of a few mgm. per liter of glucose or other utilizable organic matter the bacteria

rapidly multiply until there are several billion per ml. of enriched lake water, and the oxygen is quickly depleted.

Of secondary importance is the possibility that the individual cells exhibit the greatest respiratory activity during the early logarithmic phase of growth which occurs during the first 24 hours. Working with enriched media Martin (1932) noted the greatest oxygen consumption by *Escherichia coli* just at the end of the lag phase or about two hours after the start of his experi-

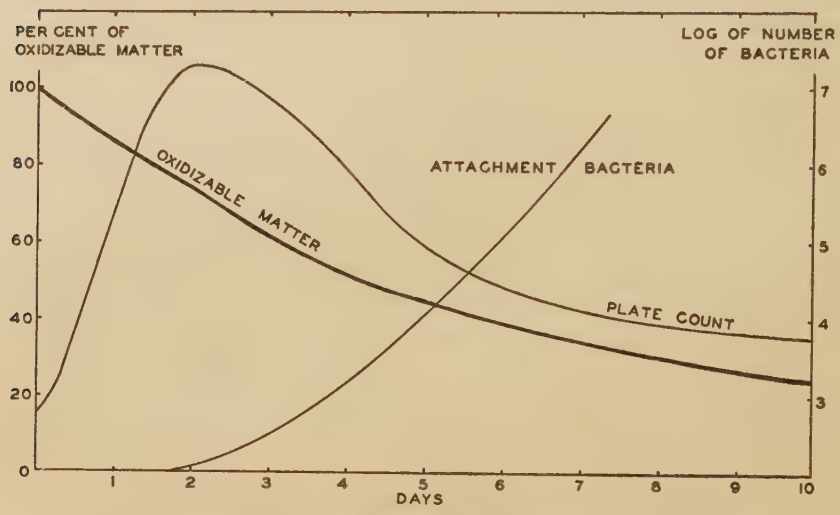


FIG. 2. BACTERIAL AND ORGANIC MATTER CONTENT OF LAKE WATER

The number of attachment bacteria per ml. of water was estimated by counting microscopically those attached per unit area of glass slide submerged in the water and multiplying by the total area of glass exposed to the water (ZoBell and Allen, 1935). The per cent of oxidizable (by bacteria) organic matter is calculated upon a basis of the biochemical oxygen demand of the water in 30 days at 25°C. being 100 per cent.

ment. Thereafter, even during the logarithmic phase, the rate of oxygen consumption per cell decreased. Similarly Clifton and Logan (1939) found that *E. coli* cells 2 to 3 hours old used 438×10^{-12} mgm. of oxygen per cell per hour while 9 to 10-hour old cells used only 9.8×10^{-12} mgm. per hour. Martin (1932) believes that the respiratory capacity of bacteria is proportional to their surface area and this is usually greatest at the end of the lag phase.

The increase in the rate of oxygen consumed per cell on the fourth and fifth days is an artifact. During this period the rate of total oxygen consumption is decreasing but the number of bacteria demonstrated by plate counts is decreasing proportionately much faster, which makes it appear that each respiring cell is consuming more oxygen. Actually there are numerous respiring bacteria tenaciously attached to the walls of the glass bottles which are not detected by plate counts. The direct microscopic observation of glass slides submerged in stored water and other evidence reviewed elsewhere (ZoBell, 1936) shows that after a day or two there are many more such attached bacteria per unit volume of stored water than in the water itself. These relationships are shown by figure 2. The respiratory capacity of these attached bacteria can be demonstrated by carefully decanting all of the water from the bottles after the fourth or fifth day of incubation and replacing it with sterile water. The periodic determination of oxygen reveals that oxygen consumption continues at an uninterrupted rate which in many cases is even faster than that in the decanted water stored in new bottles.

EXPERIMENTS WITH RESTING CELLS

The foregoing experiments indicate that the rate of respiration of lake bacteria is independent of the oxygen tension of the water although the latter influences bacterial multiplication. However, in view of the fact that the changing bacterial population is indeterminate and oxidizable organic matter becomes a limiting factor, it is questionable if the data on the respiratory capacity of the bacteria are valid except perhaps during the first 24-hour period. In order to circumvent these difficulties the respiratory rate of resting cells was studied over short periods of time in lake water enriched with oxidizable material.

The bacteria were grown on nutrose agar in prescription bottles and washed off with sterile lake water. Enough of the resulting suspension was added to lake water to give several billion viable cells per ml. The lake water was enriched by the addition of 100 mgm. per liter each of glucose, glycerol and sodium bicarbonate. Tank nitrogen was bubbled through 3-liter portions of the inoc-

ulated enriched water until the oxygen tension was reduced to approximately the desired level, as judged from experience and substantiated by trial analyses. The water was immediately siphoned into glass-stoppered bottles under nitrogen. Two samples were analyzed at once and the others placed in the water-bath at 25°C. Since the water could be bottled in less than five minutes, respiration caused little difference in the oxygen content of the first and last bottles filled with water during this interim. Duplicate bottles were analyzed at hourly intervals. *Serratia rubida* and *Flavobacterium flavus*, two bacteria found in Lake Mendota, as well as mixed cultures from the lake were studied. The results of such an experiment with *S. rubida* are

TABLE 4

Influence of oxygen tension on oxygen consumption by Serratia rubida during different periods of time at 25°C.

INITIAL OXYGEN	OXYGEN CONSUMED PER HOUR DURING				
	1st hour	2nd hour	3rd hour	4th hour	5-7th hour
mgm. per liter	*mgm. per liter*	*mgm. per liter*	*mgm. per liter*	*mgm. per liter*	*mgm. per liter*
0.30	0.08	0.07	0.10	(0.05)	(0)
0.92	0.12	0.10	0.09	0.07	0.04
2.02	0.09	0.06	0.12	0.06	0.07
4.14	0.10	0.10	0.07	0.08	0.03
8.12	0.08	0.11	0.08	0.10	0.05

summarized in table 4. Similar results were obtained with the other organisms.

It is noteworthy that, within the limits of experimental error, the rate of respiration of the resting bacteria was independent of the oxygen tension of the water. Furthermore, about the same amount of oxygen was consumed during each of the first three one-hour periods. The respiratory rate decreased after three hours but later increased until the oxygen was completely depleted from all water samples after 24 hours. This changing respiratory rate is believed to be a growth phase phenomenon; a diminution in the number of respiring cells followed by an increase.

In similar experiments with *S. rubida* and *F. flavus*, in which multiplication was inhibited with 0.1 per cent phenol, the rate

of respiration decreased progressively after the first hour or two. The phenol as well as the same concentration of formaldehyde seemed to interfere with the respiratory mechanism of the resting cells right from the first. This is evident from the data in table 5 which show the amount of oxygen consumed per cell with and without preservatives during the first hour of the experiment.

TABLE 5

Effect of preservatives on the respiration of Serratia rubida and Flavobacterium flavus

ORGANISM	PRESERVATIVE	OXYGEN CONSUMED PER CELL PER HOUR
		mgm.
Serratia rubida	None	214×10^{-12}
Serratia rubida	0.1% phenol	43×10^{-12}
Serratia rubida	0.1% formaldehyde	8.5×10^{-12}
Flavobacterium flavus	None	69×10^{-12}
Flavobacterium flavus	0.1% phenol	14×10^{-12}
Flavobacterium flavus	0.1% toluol	41×10^{-12}

TABLE 6

Oxygen uptake of lake bacteria (resting cells) in water containing different concentrations of dissolved oxygen

INITIAL OXYGEN	OXYGEN CONSUMED AFTER			
	1 hour	2 hours	4 hours	7 hours
mgm. per liter	*mgm. per liter*	*mgm. per liter*	*mgm. per liter*	*mgm. per liter*
8.52	0.92	1.69	2.95	7.29
11.12	1.04	1.55	2.62	7.36
13.98	0.98	1.58	2.83	7.42
19.35	0.83	1.81	2.38	7.05
34.52	0.92	1.78	3.09	6.99

The values are not strictly comparable because the results were obtained in different experiments not run simultaneously.

In the foregoing experiments only those oxygen tensions have been used which one might expect to find normally in natural waters. However, under special and rare circumstances 20 to 30 mgm. per liter of oxygen may occur in lake water (Birge and Juday, 1911). Therefore the effect of supersaturations of dissolved oxygen on bacterial respiration was investigated. Sterile lake water enriched with 0.1 per cent glucose was inoculated with

a heavy suspension of washed resting cells. A portion of the inoculated water was washed with oxygen until the water contained around 35 mgm. per liter of oxygen. Part of this supersaturated (with respect to the normal atmosphere) water was bottled immediately and part was diluted with remaining portions of the inoculated water to give oxygen tensions ranging from 8 to 35 mgm. per liter. The oxygen content of part of the bottled water was determined immediately and the rest was analyzed after different periods of incubation in the water-bath at 25°C. The data are summarized in table 6. Similarly, in another experiment in which the oxygen tension ranged from 7.56 to 36.48 mgm. per liter, it was found that within the limits of experimental error the oxygen uptake of lake bacteria is independent of the oxygen tension.

DISCUSSION

The values for the amount of oxygen consumed per cell may be somewhat too high because there are probably more bacteria respiring than the number indicated by the plate counts. Bere (1933) records that direct microscopic counts revealed the presence of from 20 to 235 times as many bacteria in lake water as could be demonstrated by plate counts, an observation amply confirmed by the work of others. However, we have no good method for estimating what proportion of the direct-count population consists of cells capable of respiration, while unquestionably every colony which develops on agar plates represents at least one respiring bacterium. This, together with the fact that direct-count data on a given sample are less reproducible than those obtained by plate counts, justifies the use of the latter in respiration studies until more reliable enumeration procedures become available.

Although the foregoing results indicate that the oxygen tension *per se* does not influence the rate of bacterial respiration, it is not to be inferred that this generalization applies to bacteria under all conditions. In fact, it has been found that with heavy suspensions of bacteria ($>10 \times 10^9$ per ml.), with concentrated nutrient solutions or with menstruums rich in particulate matter,

oxygen becomes a limiting factor while there is still some oxygen present. It is believed that all of the oxygen is depleted in the immediate vicinity of the respiring cells especially when the latter occur in clumps or in otherwise highly localized areas. In other words, in these localized areas oxygen may be consumed faster than it can be replaced by diffusion. Under such conditions, increasing the oxygen tension increases the oxygen gradient and hence may provide for the replenishment of oxygen as fast as it is consumed. This is quite evident in respirometers which are inadequately agitated so that the oxygen tension of the menstruum is not in equilibrium with the atmosphere and an actual lack of oxygen in the bottom of the respirometer chamber may limit respiration although the manometer indicates the presence of oxygen. Another example of the effect of high oxygen tension on the oxygen gradient is in certain industrial processes where oxygen under several atmospheres of pressure or oxygen bubbled through the vats has been found to favor aerobic transformations.

Rashevsky (1933) has expressed the opinion that the true rate of oxygen consumption by protoplasm is independent of the oxygen tension, any differences being attributable to the diffusion or penetration rate of oxygen. This is in conformity with Shoup's (1929) conclusion that oxygen consumption by small cells occurs at a "constant and maximum" rate when oxygen reaches the oxidative catalyst of the cell. Rashevsky (1933) points out that the diffusion coefficient of oxygen for different membranes may differ. Is it possible that such differences in membrane permeability may account for the higher oxygen tensions required for the maximum respiration of *Azotobacter* (Burk, 1930b, Meyerhof and Schulz, 1932), Rhizobia (Georgi and Wilson, 1933) pneumococci (Schlayer, 1936) and certain other bacteria?

According to Schlayer (1936) Type I Pneumonococci require from 20 to 30 per cent oxygen for optimum respiration although the respiration of *Escherichia coli, Pscudomonas pyocyanea, Vibrio metchnikovi* and *Staphylococcus aureus* is independent of the oxygen tension down to less than one per cent oxygen. Schlayer attributes the difference to differences in the respiratory metabolism of the pneumococci.

Upon noting that somewhat more oxygen is consumed by bacteria in sea water saturated with oxygen than in water containing less oxygen, a difference which was more pronounced when the organic residue was highly refractory to bacterial decomposition, Waksman and Renn (1936) suggest that the effect of the oxygen tension may be a function of the susceptibility of the substrate to oxidation.

Under certain conditions the oxygen tension of the medium may influence the oxidation-reduction potential and some of our observations in highly poised media suggest that the oxidation-reduction potential is a factor which influences the respiration of bacteria. Thus, under certain conditions the oxygen tension may have an indirect effect on bacterial respiration. This is being studied further.

SUMMARY

Although the oxygen tension of lake water influences the multiplication of lake bacteria, their respiration is independent of the oxygen tension within the examined ranges of 0.30 to 36.48 mgm. per liter.

After a few days storage in glass-stoppered bottles there are as many or more respiring bacteria per unit of water which are tenaciously attached to the glass as in the water itself. Only the latter are detected by plate counts.

Multiplying lake bacteria were found to use 51 to 93 $\times 10^{-12}$ mgm. of oxygen per cell per hour at 25°C. during the first day in stored lake water; but much less thereafter as oxidizable organic matter becomes a limiting factor.

Resting cells of *Serratia rubida*, *Flavobacterium flavus* and other lake bacteria were found to use from 69 to 214 $\times 10^{-12}$ mgm. of oxygen per cell per hour in lake water enriched with glucose and glycerol. Their respiration was inhibited by preservative concentrations of phenol, formaldehyde and toluol.

The authors acknowledge with gratitude the encouragement and helpful criticisms of Dr. E. A. Birge, Dr. Chancey Juday, Dr. Elizabeth McCoy, Prof. E. G. Hastings, Dr. E. B. Fred and other members of the Limnological Laboratory and the Department of Agricultural Bacteriology of the University of Wisconsin.

REFERENCES

AMBERSON, W. R. 1928 The influence of oxygen tension upon the respiration of unicellular organisms. Biol. Bull., **55**, 79–91.

BERE, RUBY 1933 Numbers of bacteria in inland lakes of Wisconsin as shown by the direct microscopic method. Intern. Rev. ges. Hydrobiol. Hydrog., **29**, 248–263.

BIRGE, E. A., AND JUDAY, C. 1911 The inland lakes of Wisconsin. I. The dissolved gases of the water and their biological significance. Wisconsin Geol. and Nat. Hist. Survey Bull., **22**, 1–259.

BUCHANAN, R. E., AND FULMER, E. I. 1930 Physiology and Biochemistry of Bacteria. Williams & Wilkins Co., Baltimore, Vol. 3, 154.

BURK, D. 1930a The influence of nitrogen gas upon the organic catalysis of nitrogen fixation by *Azotobacter*. J. Phys. Chem., **34**, 1174–1194.

BURK, D. 1930b The influence of oxygen gas upon the organic catalysis of nitrogen fixation by *Azotobacter*. J. Phys. Chem., **34**, 1195–1209.

CLIFTON, C. E., AND LOGAN, W. A. 1939 On the relation between assimilation and respiration in suspensions and in cultures of *Escherichia coli*. J. Bact., **37**, 523–540.

GEORGI, C. E., AND WILSON, P. W. 1933 The influence of the tension of oxygen on the respiration of *Rhizobia*. Arch. Mikrobiol., **4**, 543–564.

HARVEY, E. N. 1928 The oxygen consumption of luminous bacteria. J. Gen. Physiol., **11**, 469–475.

HENRICI, A. T., AND MCCOY, ELIZABETH 1938 The distribution of heterotrophic bacteria in the bottom deposits of some lakes. Trans. Wisconsin Acad. Sci., **31**, 323–361.

HEUKELEKIAN, H. 1936 Oxygen tension and bacterial numbers. Sewage Works J., **8**, 415–421.

HYMAN, LIBBIE H. 1929 The effect of oxygen tension on oxygen consumption in *Planaria* and some *Echinoderms*. Physiol. Zool., **2**, 505–534.

KUSNETZOW, S. E. 1935 Microbiological researches in the study of the oxygen regimen of lakes. Verhandl. Intern. Ver. theor. angew. Limnologie, **7**, 562–582.

MARTIN, D. S. 1932 The oxygen consumption of *Escherichia coli* during the lag and logarithmic phases of growth. J. Gen. Physiol., **15**, 691–708.

MEYERHOF, O., AND SCHULZ, W. 1932 Über die Abhängigkeit der Atmung der *Azotobacter* vom Sauerstoffdruck. Biochem. Z., **250**, 35–49.

NOVY, F. G., AND SOULE, M. H. 1925 Microbic respiration. II. Respiration of the tubercle bacillus. J. Infectious Diseases, **36**, 168–232.

POMEROY, R. 1938 Influence of oxygen concentration on biochemical oxygen demand. Sewage Works J., **10**, 465–472.

PÜTTER, A. 1924 Die Atmung der Planktonbakterien. Pflügers Arch. ges. Physiol., 204, 94–126.

RASHEVSKY, N. 1933 Note on the mathematical theory of oxygen consumption at low oxygen pressures. Protoplasma, **20**, 125–130.

SCHLAYER, E. 1936 The influence of oxygen tension on the respiration of *Pneumococci* (Type I). J. Bact., **31**, 181–189.

SHOUP, C. S. 1929 The respiration of luminous bacteria and the effect of oxygen tension upon oxygen consumption. J. Gen. Physiol., **13**, 27–45.

STEPHENSON, M., AND WHETHAM, M. 1924 The effect of oxygen supply on the metabolism of *Bacillus coli communis*. Biochem. J., **18,** 498–506.

WAKSMAN, S. A., AND CAREY, C. L. 1935 Decomposition of organic matter in sea water by bacteria. I. Bacterial multiplication in stored sea water. J. Bact., **29,** 531–543.

WAKSMAN, S. A., AND RENN, C. E. 1936 Decomposition of organic matter in sea water by bacteria. III. Factors influencing the rate of decomposition. Biol. Bull., **70,** 472–483.

WARBURG, O., AND KUBOWITZ, F. 1929 Atmung bei sehr kleiner Sauerstoffdrucken. Biochem. Z., **214,** 5–18.

WOHLFEIL, T. 1930 Ueber die Abhängigkeit der Atmungsintensität atmender Bakterienaufschwemmungen von der Bakterienzahl. Zentr. Bakt. Parasitenk., I Abt., Orig., **117,** 202–212.

ZOBELL, C. E., AND ANDERSON, D. Q. 1936 Observations on the multiplication of bacteria in different volumes of stored sea water and the influence of oxygen tension and solid surface. Biol. Bull., **71,** 324–342.

ZOBELL, C. E. 1936 Periphytic habits of some marine bacteria. Proc. Soc. Exptl. Biol. Med. **35,** 270–273.

ZOBELL, C. E., AND ALLEN, ESTHER C. 1935 The significance of marine bacteria in the fouling of submerged surfaces. J. Bact., **29,** 239–251.

Contribution No. 90

ON THE ANNUAL AND DIURNAL VARIATION OF THE EVAPORATION FROM THE OCEANS*

By

H. U. SVERDRUP

Scripps Institution of Oceanography
University of California
La Jolla, California

The average annual evaporation of the oceans in different latitudes can be considered fairly well established (Mosby, 1936, Wüst, 1936), but so far little is known as to the character of the annual and the diurnal variations. Helland-Hansen (1930) has pointed out that evaporation will be facilitated if the sea surface is warmer than the air, whereas evaporation will decrease or cease if the sea surface is colder. He has therefore concluded that in middle latitudes the evaporation is at a maximum in fall and early winter, and at a minimum in summer, and, similarly, it may be concluded that the evaporation is at a maximum during the night and is somewhat smaller in the middle of the day. It will here be attempted to approach the problem on the basis of energy considerations which have been applied successfully in the study of the average evaporation from the sea (W. Schmidt, 1915), and of the evaporation from reservoirs and lakes (Ångström, 1920, Cummings and Richardson, 1927). A few specific examples will be discussed and a few conclusions will be drawn.

In this case, the energy equation states that the total amount of heat lost from a square unit of surface area in unit time, q_a, partly

* Contributions from the Scripps Institution of Oceanography, New Series, Number 90.

Reprint from SEARS FOUND. JOURN. MAR. RES.

as heat used for evaporation, q_e, and partly as sensible heat given off to the atmosphere, q_c, must equal the difference between the surplus radiation (radiation from sun and sky minus effective back radiation from the sea surface) which is absorbed by the water, q_r, and the time change of the heat content of the water:

$$q_e + q_c = q_r - \int_0^\infty \frac{d}{dt}(c\rho\tau)\, dz \tag{1}$$

Here c, ϱ, and τ mean specific heat, density and temperature, respectively. The amount of heat given off to the atmosphere by convection is generally assumed to be a small fraction of q_e, and $q_a = q_e + q_c$ represents, therefore, approximately the amount of heat used for evaporation.

The surplus of radiation can be found either by means of Kimball's data (1928) or Mosby's formula (1936), taking into account reflection at the surface and using Ångström's results (1920) as to the effective back radiation. Evaluation of the integral

$$\int_0^\infty \frac{d}{dt}(c\rho\tau)dz = c\rho\left[\int_0^\infty \frac{\partial\tau}{\partial t}dz + \int_0^\infty v_x\frac{\partial\tau}{\partial x}dz + \int_0^\infty v_y\frac{\partial\tau}{\partial y}dz + \int_0^\infty v_z\frac{\partial\tau}{\partial z}dz\right] \tag{2}$$

is generally more difficult, because it necessitates knowledge of the temperature changes within a given water mass. In certain instances approximately correct values can be determined.

ANNUAL VARIATION OF EVAPORATION

Helland-Hansen (1930) has pointed out that water masses of different origin may be carried into the area under examination, for which reason the observed temperature changes may be related to variations in the character of the water masses present and not to processes of heating or cooling. In order to overcome this difficulty, Helland-Hansen examined the "temperature anomalies" as defined by means of deviations from standard T-S curves, and on this basis he arrived at a series of curves showing the effect of heating in three areas of the eastern North Atlantic, the data being relatively complete for an area off the Bay of Biscay, with its center at 47° N. and 12° W. The data are from a region without very distinct currents, for which reason only the first term on the right-hand side of equation (2) has to be considered, and this can be computed from Helland-Hansen's data, introducing $c = 0.93$ and $\varrho = 1.025$. Thus, the curve marked q_τ in Figure 31A was obtained, showing the variation during the year of the

amount of heat involved in heating or cooling the water, and expressed in gm. cal./cm.^{2} min. Kimball gives values of the total incoming radiation on the 21st of every month of the year at 48° N., 4° W., and the effective back radiation in this locality can be obtained by means of Ångström's table using the same values of cloudiness which were used by Kimball in his computation. Thus, the curve marked q_r

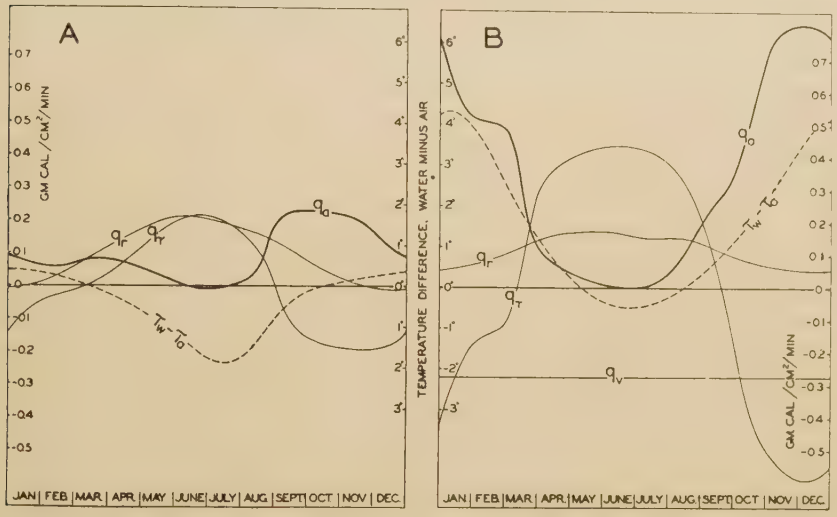


Figure 31. A. Annual variation of evaporation off the Bay of Biscay, in about 47° N. and 12° W. Curve q_T represents the surplus of radiation heat which is absorbed by the water, curve q_T represents the heat involved in heating and cooling the water. Curve q_a represents the heat given off to the atmosphere mainly by processes of evaporation. The curve $\tau_w - \tau_a$ represents the difference between the surface temperature of the water and the temperature of the air. B. Annual variation of evaporation within the region of the Kurosio in about 32° 40′ N. and 135° 50′ E. The designation of the curves is the same as in figure 32 A. In addition, q_v represents the loss of heat of the water due to change of temperature in the direction of flow.

is found showing the variations through the year of the radiation surplus, also expressed in gm. cal./cm.^{2}min. Assuming that the values of q_r are applicable to the same region as those of q_T, the amount of heat given off by evaporation and convection is found by subtraction of the two curves and is represented by curve q_a in Figure 31A.

The curve q_a represents roughly the annual variation of evaporation, and this computation leads therefore to the result that the evaporation is great from the middle of September to the middle of December, is small from January to May, and ceases in June and July. It is of particular interest to observe that a secondary minimum of evaporation appears to occur in February and that apparently the

increase of radiation surplus in early spring is accompanied by an increase in evaporation leading to a secondary maximum in March.

In the figure, the curve marked $\tau_w - \tau_a$ represents the temperature difference between the water and the air as derived from the charts for seasons in the Atlas of Climatological Charts (1939). The agreement between this curve and the curve q_a is good, as should be expected from Helland-Hansen's reasoning. Assuming that in this case 90% of the total heat loss is used for evaporation, one obtains that in late fall the daily evaporation amounts to about 0.5 cm. and the total annual evaporation to about 81 cm.

A similar method has been applied to the region south of Japan, using data concerning the annual variation of temperature in the waters of the Kurosio in about 32° 40′ N. and 135° 50′ E. At stations located along a line running due south from Siono-misaki, about 100 miles long and extending from 33° 30′ N. to 31° 50′ N., the annual variation of temperature was examined by Suda on the basis of observations from 1923 to 1927. The observations which were taken in the N.E.-flowing branch of the Kurosio have been re-examined by Koenuma (1939), whose tables have been used here.

The radiation income in this area can be derived from Kimball's data. If, in this case, one introduces

$$q_\tau = c\rho \int_0^\infty \frac{\partial \tau}{\partial t}\, dz$$

one arrives at the result that in summer large amounts of heat are taken up from the atmosphere. This appears unreasonable and must be due to the fact that the other terms in (2) can not be neglected, because in this region a distinct current exists within which the temperature decreases in the direction of flow. It is not known how great this decrease is, nor whether it is independent of the seasons, but for the sake of simplicity it will be assumed that the term

$$q_v = c\rho \int_0^\infty v_x \frac{\partial \tau}{\partial x} dz$$

is constant throughout the year and so great that in summer q_a becomes zero and that other terms can be omitted. Figure 32B shows the curves q_r, q_τ, and q_v, and

$$q_a = q_r - q_\tau - q_v$$

which approximately represents the evaporation. In this case the evaporation is at a maximum in winter, and this result appears trust-

worthy, because in winter the cold and dry monsoon blows from the Asiatic Continent.

In November, December, and January an average of .750 gm. cal./cm.^{2} min. is given off to the atmosphere. Of this amount three-fourths or more is given off as latent heat of water vapor corresponding to an evaporation of about 1.4 cm. per day. On a similar basis the total evaporation in one year would amount to 266 cm. which is more than twice Wüst's average value in that latitude, 116 cm. per year. The difference indicates that the evaporation is greatest near the west-

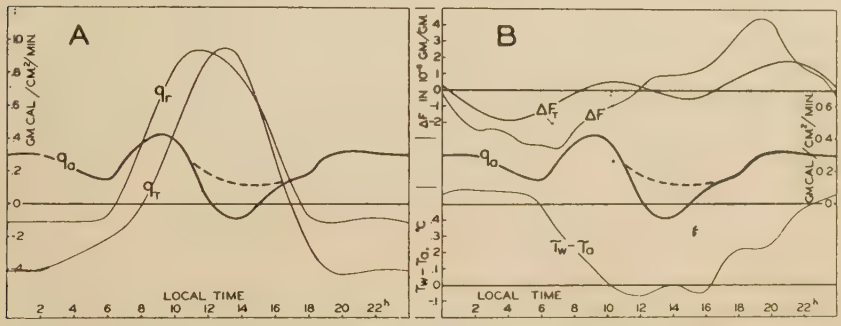


Figure 32. A. Diurnal variation of evaporation in the tropics, according to observations on four "Meteor" stations. The designation of the curves is the same as in figure 32A. B. The curve q_a represents the diurnal variation of heat given off to the atmosphere at four "Meteor" stations, the curves $\tau_w - \tau_a$ and ΔF represent the difference between water-surface temperature and air temperature, and the diurnal variation of the specific humidity of the air on the same four days. The curve ΔF_T represents the diurnal variation of the specific humidity of the air on 18 selected days in the tropics, according to Reger.

ern border of the North Pacific Ocean, as may be expected when the character of the currents and the atmospheric circulation is considered.

The temperature difference, water minus air, which is also shown in the figure as derived from the Atlas of Climatological Charts of the Oceans, varies as the computed evaporation and in winter is greater near Japan than anywhere else in the Pacific Ocean.

In the part of the Kurosio under consideration, one may perhaps assume that the velocity between the surface and 200 meters is 50 cm./sec. With this value of v one finds that the value of q_v which was introduced corresponds to a decrease of the temperature of 0.2° C. in the upper 200 meters on a distance of about 400 km. It is impossible to verify this conclusion because the change in temperature in the direction of flow of the Kurosio appears to be mainly caused by admixture of colder water. The estimated cooling due to the

amount of heat given off to the atmosphere appears, however, to be conservative.

DIURNAL VARIATION OF EVAPORATION IN THE TROPICS

In order to examine the diurnal variation of evaporation by means of the same method it is necessary to know the diurnal variation of temperature at different depths. From the tropics the observations at four of the "Meteor" anchor stations give the necessary information. These data have been examined by Defant (1932) who, from the decrease of amplitude and change of phase of the diurnal variation of temperature at the surface and at 50 meters, concluded that the eddy conductivity was constant in the upper homogeneous layer which had a thickness of about 70 meters. This implies that the diurnal variation of temperature at a depth z can be expressed by means of a sum of harmonic terms,

$$\tau = \Sigma A_n e^{-\kappa_n z} \sin\left(n\frac{2\pi}{T}t + \alpha_n - \kappa_n z\right)$$

where A_n represents the amplitude of the nth term at the surface, α_n, the phase of that term at the surface, T, the length of the day in hours, minutes, or seconds depending upon the units used for measuring the time, and where

$$\kappa_n = \sqrt{\frac{n\pi\rho}{\eta T}}$$

Here, η is the eddy conductivity. From change of phase and reduction of amplitude Defant found $\eta = 322$ gm./cm. sec. The amount of heat used in unit time for local heating and cooling is, therefore,

$$q_\tau = c\rho\int_0^\infty \frac{\partial t}{\partial t}\,dz = \Sigma A_n \frac{n2\pi}{T}\frac{c\rho}{\kappa_n 2\sqrt{2}}\sin\left(n\frac{2\pi}{T}t + \alpha_n + \frac{\pi}{4}\right)$$

In this case it may be assumed that q_v can be neglected.

By means of the hourly values of sea-surface temperature as given by Defant the curve marked q_τ in Figure 32A has been computed, but it should be observed that the amplitude of the curve is subject to some uncertainty because it depends upon the accuracy of the value of η. Taking into account the location of the stations, the dates on which they were occupied, and the average hourly values of cloudiness, as stated in the tables of meteorological observations (Kuhlbrodt and Reger, 1938), the curve q_r has been computed by means of

Mosby's formula and the Ångström values of back radiation. The difference between these two curves, q_a, represents the amounts of heat given off in unit time to the atmosphere by convection or lost by evaporation. It may again be assumed that the heat used for evaporation is considerably greater than that given off by convection, and that the curve q_a, therefore, roughly represents the diurnal variation of the evaporation.

In the tropics the diurnal variation of evaporation appears to be somewhat similar in character to the annual variation in middle latitudes in the eastern North Atlantic. The maximum evaporation takes place during the early hours of the night, falls off during the latter part of the night towards a secondary minimum in the early morning, rises sharply when the sun appears above the horizon, but drops again to a low minimum in the early afternoon hours. Thus, a semi-diurnal period appears more pronounced than a diurnal, but it is possible that, owing to uncertainties as to the amplitudes of q_r and q_τ, the afternoon minimum, as indicated by the dashed part of the curve q_a, appears too low in this special case. The total evaporation in one day is about 0.5 cm.

It is possible to point out certain observations which substantiate the conclusion that in the tropics a semi-diurnal period prevails. In general, q_r can be expressed as the sum of a constant term and a series of harmonic terms,

$$q_r = \bar{q}_r + \Sigma b_n \sin\left(n\frac{2\pi}{T}t + \beta_n\right)$$

and, similarly, q_τ, can be expressed as a series of harmonic terms,

$$q_\tau = \Sigma a_n \sin\left(n\frac{2\pi}{T}t + \alpha_n + \frac{\pi}{4}\right)$$

Therefore,

$$q_a = \bar{q}_r + \Sigma c_n \sin\left(n\frac{2\pi}{T}t + \gamma_n\right)$$

where

$$c_n = \sqrt{a_n^2 + b_n^2 - 2a_n b_n \cos\left(\beta_n - \alpha_n - \frac{\pi}{4}\right)},$$

$$tg\gamma_n = \frac{a_n \sin\left(\alpha_n + \frac{\pi}{4}\right) - b_n \sin\beta_n}{a_n \cos\left(\alpha_n + \frac{\pi}{4}\right) - b_n \cos\beta_n}$$

We are here interested in the variation of the evaporation and can therefore disregard the constant term. It is evident that each one of the harmonic terms will attain its minimum value if $\alpha_n = \beta_n - \pi/4$. The surplus radiation q_r is, in general, symmetrical around noon and the phase angles of the first two harmonic terms have the values $\beta_1 = 270°$ and $\beta_2 = 90°$. In the tropics, the amplitude of the second harmonic term is relatively great, but in middle latitudes it nearly disappears. It is striking that harmonic analysis of a large number of observations of sea-surface temperatures in the tropics leads to the result that $\alpha_1 = 270° - 45° = 225°$. Hann's analysis of the "Challenger" data gives 227.5, whereas Krümmel and Wegemann from other data obtain 223.8 and 225.8, respectively (Defant, 1932). This indicates that the diurnal variation of the evaporation is as small as possible. There exists, on the other hand, no agreement between the second terms. From the four days dealt with above, Defant's analysis gives $\alpha_2 = 19°$, and the studies by Krümmel and Wegemann give $\alpha_2 = 26°$ and 26.9°, respectively, instead of 45°. Therefore, it may be expected that the semi-diurnal term will be relatively larger. If we make the assumption that the amplitudes b_2 and a_2 are equal, we find that the phase angle of the semi-diurnal evaporation term is about 170°, meaning that the first minimum comes at 3.3^h and the second minimum at 15.3^h. In middle latitudes the diurnal terms dominate both in q_r and q_r (Wegemann, 1920), and it appears therefore probable that the diurnal variation of the evaporation is more prominent there, and is mainly dependent upon the difference $a_1 - b_1$, because α_1 is close to 225°.

FACTORS WHICH INFLUENCE THE DIURNAL VARIATION OF EVAPORATION

The evaporation from a water surface must, on the one hand, be nearly proportional to the difference between the surplus radiation and the heat used for temperature change of the water, and on the other hand must equal the amount of water vapor which is transported upwards from the surface by processes of eddy diffusion. This upwards transport depends mainly upon the wind velocity, the difference between vapor pressure at the surface and in the air at a short distance from the surface, and the state of turbulence of the air (Sverdrup, 1937). Over the oceans the diurnal variations of the two former factors are relatively small, and it may therefore be assumed that the state of turbulence of the air is of dominant importance. It appears reasonable to assume that shortly after sunrise the turbulence will increase, for which reason the evaporation will also increase. In the tropics

the increase will not continue unimpeded, however, because towards noon the air temperature may become higher than that of the temperature of the sea surface, the stratification becomes stable and the turbulence will be reduced in the early hours of the afternoon. In the late afternoon when the air temperature has dropped below that of the surface, the turbulence will again increase and will reach a maximum some time after sunset. Such a diurnal variation of the turbulence would account for the double period of the evaporation in the central part of the tropics, but in the trade-wind areas and in middle latitudes the air temperature remains below that of the water, and in these circumstances turbulence does not decrease at noon. There, a single period of the evaporation should be expected, probably with minimum in the early forenoon when the temperature difference, water minus air, is smallest (Kuhlbrodt and Reger, 1938). It may be pointed out that over land the evaporation in low latitudes appears to have a single diurnal period with its minimum value at sunrise and its maximum value in the early afternoon. Such a period is in agreement with the fact that over land the surface is warmer than the air throughout the day, and the turbulence has its maximum in the early afternoon hours.

THE DIURNAL VARIATION OF EVAPORATION AND OF THE SPECIFIC HUMIDITY OF THE AIR IN THE TROPICS

In Figure 32B are shown the computed diurnal variations of the heat given off to the atmosphere, q_a, at the four "Meteor" stations, and curves representing the hourly deviations of the specific humidity from the average value, ΔF, and the difference between water and air temperature, $\tau_w - \tau_a$. The minimum of evaporation in the early afternoon hours appears, as was pointed out, to be associated with the fact that in these hours the water was colder than the air, for which reason the turbulence and, consequently, the upwards transport of water vapor was reduced.

The variation of the specific humidity of the air, ΔF, indicates, on the other hand, the presence of a semi-diurnal period which is slightly displaced in relation to the evaporation. These curves are all based on observations from the four days only, but in his discussion of the meteorological observations from the "Meteor," Reger points out that in the tropics the specific humidity shows a pronounced semi-diurnal variation with minima about 4^h and 15^h, and maxima at 10^h and 21^h. Reger's general curve for the tropics is also entered in the figure, and is marked ΔF_T.

If the results as to the evaporation which have been obtained by our example can be generalized it appears that there is a close correspondence between the diurnal variation of the evaporation and that of the specific humidity of the air, as may be expected from a consideration of the processes involved. Variations of the specific humidity in a cube of air at a short distance from the sea surface depend upon the difference between the supply of water vapor through the lower horizontal surface of the cube and the upwards transport of water vapor through the upper horizontal surface. Near the sea surface differences in transport through the vertical surfaces of the cube can be neglected, and if the upwards transport of water vapor associated with the turbulence of the air were constant, the specific humidity would not vary. If now the evaporation increases but the upwards transport remains unaltered the specific humidity must increase. Suppose next that the increase of the evaporation stops so that the supply of water vapor reaches a new but higher value than previously. Then the specific humidity will a little later become constant but will have attained a somewhat higher value. When the evaporation decreases similar considerations are applicable and one is therefore led to the conclusion that under these conditions the specific humidity must vary as the evaporation, but the minima and maxima of the specific humidity must come some time after the corresponding extreme of evaporation. Similarly, a decrease in the upwards transport must lead to an increase of the specific humidity if the evaporation remains constant. Present knowledge of variations of the evaporation and the state of turbulence is too scanty to permit a further examination of the question, but in the tropics the agreement between the variations of the evaporation and the specific humidity is so striking that it appears worth while pointing out. In the trade-wind area a single diurnal period of the specific humidity dominates and there the semi-diurnal period in the evaporation should be expected to be small.

SUMMARY

The annual variation of evaporation is examined by means of the energy equation in an area off the Bay of Biscay and in a part of the Kurosio off southern Japan. In both areas maximum evaporation appears to take place in late fall or early winter, the evaporation in the Kurosio area being nearly three times that off the Bay of Biscay. In both areas the evaporation ceases in summer, but off the Bay of Biscay a secondary maximum occurs in March.

The diurnal variation of evaporation in the tropics is examined in a similar manner. A semi-diurnal period is found which is explained as a result of the varying state of turbulence and which appears to throw light on the previously established semi-diurnal variation of the specific humidity of the air.

LITERATURE

Ångström, A.

1920. Application of heat radiation measurements to the problems of the evaporation from lakes and the heat convection at their surfaces. Geogr. Ann., Heft 3, 16 pp., 1920.

Cummings, N. W., and Burt Richardson.

1927. Evaporation from lakes. Phys. Rev., vol. 30, p. 527–34, 1927.

Defant, A.

1932. Die Gezeiten und internen Gezeitenwellen des Atlantischen Ozeans. Wiss. Erg. d. "Meteor"-Exped., Bd. 7, Teil 1, 318 pp., 1932.

Helland-Hansen, B.

1930. Physical oceanography and meteorology. Rept. Sci. Results of the "Michael Sars" North Atlantic Deep-Sea Expedition, 1910., vol. 1, 102 pp., Bergen, 1930.

Kimball, H.

1928. Amount of solar radiation heat that reaches the surface of the earth on the land and on the sea. Monthly Wea. Review, vol. 56, pp. 393–98, 1928.

Koenuma, K.

1939. On the hydrography of the southwestern part of the North Pacific and the Kurosio. Imperial Marine Observ., Kobe, Japan, Memoirs, vol. 7, pt. 3, pp. 41–113, 1939.

Kuhlbrodt, E., und J. Reger.

1938. Die meteorologischen Beobachtungen. Wiss. Erg. d. "Meteor"-Exped., Bd. 14, 392 pp., Berlin, 1938.

Mosby, H.

1936. Verdunstung und Strahlung auf dem Meere. Ann. d. Hydr. u. mar. Met., Bd. 54, p. 281–286, 1936.

Schmidt, W.

1915. Strahlung und Verdunstung an freien Wasserflächen. Ann. d. Hydr. u. mar. Met., Bd. 43, pp. 111–24, 169–78, 1915.

Sverdrup, H. U.

1937. On the evaporation from the oceans. Jour. Marine Research, vol. 1, pp. 3–13, 1937.

U. S. Weather Bureau.

1938. Atlas of climatic charts of the oceans. W. B. no. 1247, 1938.

Wegemann, G.

1920. Der tägliche Gang der Temperatur der Meere, usw. Wiss. Meeresuntersuchungen, Abt. Kiel, vol. 19, p. 51–85, 1920.

Wüst, G.

1936. Oberflächensalzgehalt, Verdunstung, und Niederschlag auf dem Weltmeere. Länderkundliche Forschung, Festschrift Norbert Krebs, p. 347–59, 1936.

Contribution No. 91

B.A.N.Z.
ANTARCTIC RESEARCH EXPEDITION
1929-1931

UNDER THE COMMAND OF DOUGLAS MAWSON, Kt., O.B.E., B.E., D.Sc., F.R.S.

REPORTS—SERIES A

EDITED BY SIR DOUGLAS MAWSON, UNIVERSITY OF ADELAIDE

VOLUME III

(Oceanography)

PART 2

HYDROLOGY

SECTION II

DISCUSSION

By H. U. SVERDRUP

Author's Reprint.

ADELAIDE

PUBLISHED BY THE B.A.N.Z.A.R. EXPEDITION COMMITTEE

and issued through the Barr Smith Library, University of Adelaide

Printed at The Hassell Press

January, 1940

Price eleven shillings and sixpence sterling (post free)

ALL RIGHTS RESERVED

Wholly set up and printed in Australia at The Hassell Press, Adelaide.
Registered at the General Post Office, Adelaide, for transmission through the post as a book

REPORTS OF B.A.N.Z. ANTARCTIC RESEARCH EXPEDITION, 1929-1931

SERIES A.

			s. sterling (post free)	d.
Vol. I.		Geographical Report (in preparation)		
Vol. II.	Part 1.	Rocks from Enderby Land. *By C. E. Tilley*	4	0
	Part 2.	Rocks from MacRobertson Land. *By C. E. Tilley*		
	Part 3.	The Petrology of Heard Island. *By G. W. Tyrrell*	5	0
	Part 4.	The Petrology of Possession Island (Crozets). *By G. W. Tyrrell*		
	Part 5.	The Tertiary Lavas of Kerguelen Island. *By A. B. Edwards*	5	0
	Part 6.	Marine Tertiary Fossils from Kerguelen Island. *By H. O. Fletcher*	3	0
	Part 7.	Soils from Subantarctic Islands. *By C. S. Piper*	2	0
Vol. III.	Part 1.	Soundings, *by S. A. C. Campbell; M. H. Moyes; K. E. Oom, and the Ship's Officers*	3	6
	Part 2.	Hydrology. *By A. Howard and H. V. Sverdrup*	11	6
Vol. IV.		Meteorology, etc. (in preparation).		
Vol. V.		Glaciology (in preparation).		

SERIES B.

Vol. I.	Part 1.	Biological Organization and Station List. *By T. Harvey Johnston* (1937)	5	6
	Part 2.	Fishes. *By J. R. Norman* (1937)	5	0
Vol. II.		Birds. *By R. A. Falla* (1937)	50	0
Vol. III.		Reports on Mammals (in preparation)		
Vol. IV.	Part 1.	Collembola, *by H. Womersley*; Loricata, *by B. C. Cotton*; Brachiopoda, *by B. C. Cotton*; Coleoptera, *by H. Womersley* (1937)	5	0
	Part 2.	Cumacea and Nebaliacea, *by H. M. Hale* (1937)	3	0
	Part 3.	Diptera, *by H. Womersley*; Miscellaneous Insecta, *by H. Womersley*; Lepidoptera, *by H. Womersley and N. B. Tindale* (1937)	4	6
	Part 4.	Polychaeta, *by C. C. A. Monro* (1939)	9	6
	Part 5.	Opiliones and Araneae, *by V. V. Hickman* (1939)	4	6
	Part 6.	Crinoidea, *by D. Dilwyn John* (1939)	3	6

Other Reports are in preparation.

New Series, No. 33

PART 2

HYDROLOGY

SECTION II:

DISCUSSION

BY

H. U. SVERDRUP

CONTENTS

SECTION II.

DISCUSSION

By H. V. SVERDRUP.

		Page
1.	Introductory Remarks	89
2.	Water Masses of the Indian and Australian Antarctic Oceans	89
3.	The Antarctic Upper Water	91
4.	The Upper Water of the Subantarctic Region	95
5.	The Antarctic Intermediate Water	97
6.	The Deep Water	101
7.	The Bottom Water	105
8.	Oxygen	109
9.	Vertical Sections	112
10.	Results of Dynamical Calculation	119
11.	The Deep Water Circulation of the Oceans	123
	Literature	124
	List of Text Figures 10–36	125

HYDROLOGY

SECTION II:

DISCUSSION

By H. U. SVERDRUP,

Director of the Scripps Institution of Oceanography, California.

(Text Figures 10–36; Tables V–X.)

1. INTRODUCTORY REMARKS.

In the following discussion it will be attempted to analyse the character of the different water masses of the Indian and Australian Antarctic Ocean, and the character of the currents in this area, paying special attention to the conditions near the Antarctic Continent. Observations of temperature and salinity are most suited for this purpose, and the results of the chemical investigations will be considered only if they can give added information as to the circulation.

In Section I of this Part the hydrographer of the Expedition (Mr. A. Howard) has described the instrumental equipment, the methods of observation, and the possible errors of the final values which are given in Tables II and III. It is, therefore, unnecessary to deal further with these questions, but it shall already in this place be mentioned that the salinity observations at the southern stations of the first cruise (1929–1930) appear to be systematically too low. We shall return to this matter on a later occasion.

The values in the tables of results are these which have been communicated by Howard. In a few instances values, regarding which Howard has not entered any remark, have been considered doubtful, and omitted or changed. In such case a special note has been added. The computations of the depths by pressure thermometer have been checked. The method used by Howard for computing the actual depths of observations by means of these data could have been somewhat improved, but the data are often insufficient for a more exact computation, and since the improvement would be small no changes are made. The values of σ_t have been recomputed, and in a separate column the values of the anomalies of the specific volume have been added.

The results of current measurements are communicated by Howard, but a further analysis of these data has not been attempted since too few data are available.

2. THE WATER MASSES OF THE INDIAN AND AUSTRALIAN ANTARCTIC OCEAN.

Under the name "The Indian and Australian Antarctic Ocean", we shall understand the region between longitudes 20° E., representing approximately a line from Cape Agulhas to the Antarctic Continent, and 180° E., representing a line between a position somewhat to the east of New Zealand and the Antarctic Continent. To the south the region is bounded by the Antarctic Continent, and to the north by the sub-Tropical Convergence which follows, approximately,

the latitude of 40° S. This area is again subdivided by the Antarctic Convergence, which at the surface separates the Antarctic from the sub-Antarctic region.

The characteristic features of the water masses within these regions are known from the results of preceding expeditions, and are best recognized by means of T-S curves. In Fig. 10 T-S curves

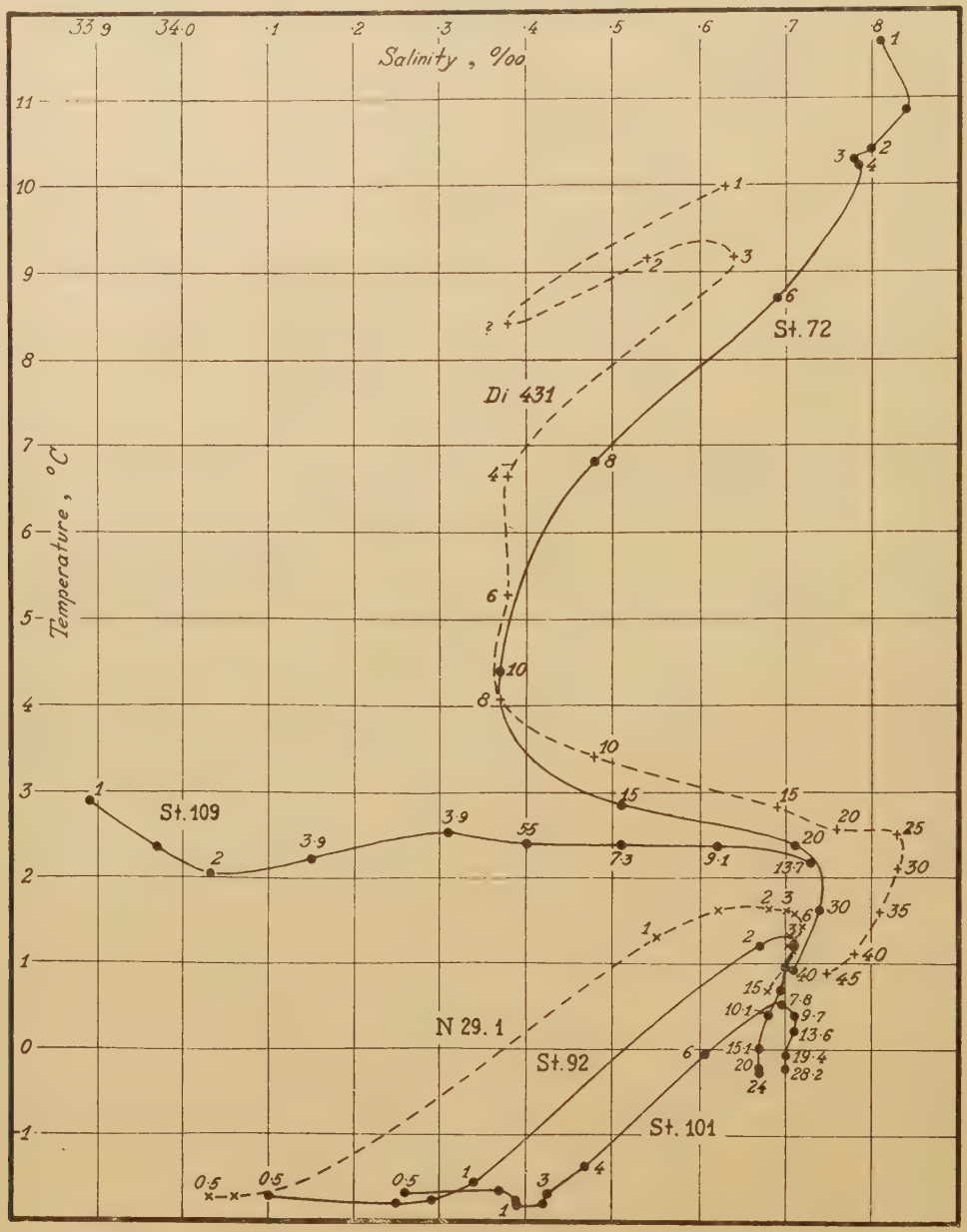


Fig. 10. Characteristic T–S curves from the Indian-Australian Antarctic Ocean.

from some characteristic B.A.N.Z.A.R.E. stations are shown; the depths of observations are entered in hectametres. Station 72 is situated within the sub-Antarctic region. Here the upper layers of sub-Antarctic water are warm and saline, but the salinity decreases with depth until a minimum is reached at about 1000 metres where the corresponding values of temperature and salinity are 4·6° and 34·37‰. This water represents the core of the Antarctic intermediate

vater. Below the intermediate water the salinity increases with depth until a maximum at about 700 metres, but below 2000 metres the variations in temperature and salinity are small. Between 000 and 4000 metres the temperature decreases from 2·3° to 0·9°, and the salinity varies be-ween 34·72 and 34·74.

Station 109 is taken nearly at the Antarctic Convergence. The intermediate water is not onspicuous, the temperature remains almost constant from 100 to 1370 metres, but the salinity ncreases regularly. No observations could be taken below 1370 metres owing to heavy swell, but t is quite evident that the almost homogeneous deep water, which at Station 72 is met with at 2000 netres, here is found from about 1300 metres and downwards.

Station 92 is situated at a short distance from the shelf of the Antarctic Continent. Down o a depth of about 100 metres the water is very cold; here we encounter the Antarctic upper vater. At 100 metres the transition to the almost homogeneous deep water begins, and from 300 netres and downwards this water is present. Station 101 lies still nearer the shelf. Here the Antarctic upper water is found down to almost 400 metres, and the deep water from about 800 netres and downwards.

The observations from two stations from other expeditions have been added. The station "Discovery II" 431 was taken within the sub-Antarctic region in 41° 58′ S., 35° 57′ E. Except or some irregularities between 100 and 400 metres it shows essentially the same feature as Sta-ion 72, which lies much further to the east. The deep water, below 2000 metres has, however, t Station Di. 431, a much higher salinity than the corresponding deep water at Station 72.

Station N, 29, 1 was taken on the "Norvegia" Expedition 1929–30 (Mosby, 1934). It is situ-ated not far from the continental shelf in 64° 15′ S., 53° 15′ E. The T-S curve is very similar o the T-S curve at Station 92 in 64° 19′ S., 116° 42′ E.

Thus, we can discriminate between the following characteristic water masses:

1. Antarctic upper water, which occurs only in the upper layers to the south of the Antarctic Convergence. This water has a low salinity, but can, according to its temperature, be divided nto two groups (Mosby, 1934): Antarctic surface water which in summer may be heated to a emperature of a few degrees above zero, and Antarctic winter water which, where it is found in an unmixed state, is at the temperature of freezing corresponding to the salinity of the water.

2. Sub-Antarctic upper water which is found between the Antarctic and sub-Tropical Con-vergences and above the Antarctic intermediate water. The water masses 1 and 2 form together he troposphere in the area in question.

3. Antarctic intermediate water which is found to the north of the Antarctic Convergence and lirectly below the sub-Antarctic upper water.

4. Deep water, which on the southern side of the Antarctic Convergence is met with at depths below 200 to 600 metres, but on the northern side at depths below 2000 metres.

5. Bottom water which has a lower temperature and a lower salinity than the deep water.

We shall examine the properties of these different water masses somewhat closer.

3. THE ANTARCTIC UPPER WATER.

At all stations to the south of the Convergence we encounter a rapid increase of the tempera-ure at the transition from the upper water to the deep water, and we may consider the depth to he layer of maximum increase as representing the thickness of the upper water. Excepted are, of course, the stations on the shelf where the upper water is present to the bottom.

The depth of the upper layer is easily determined at all stations. At some distance from the helf it is about 100 metres only, but in the immediate vicinity of the shelf it is much greater, and s, for instance, at Station 38, about 600 m. In Fig. 11 the values are plotted on a chart, and

a few lines of equal thickness are drawn, from which it is seen that the increase in thickness takes place directly outside of the continental shelf. Observations close to the shelf are not available along the whole coast, but the feature appears to be typical for the entire region between 180° E. and 60° E. Mosby (1934) has shown that the same feature was found further to west as well, except within a region between 5° E. and 10° E., where in the direct vicinity of the coast the thickness of the upper layer was only about 140 metres.

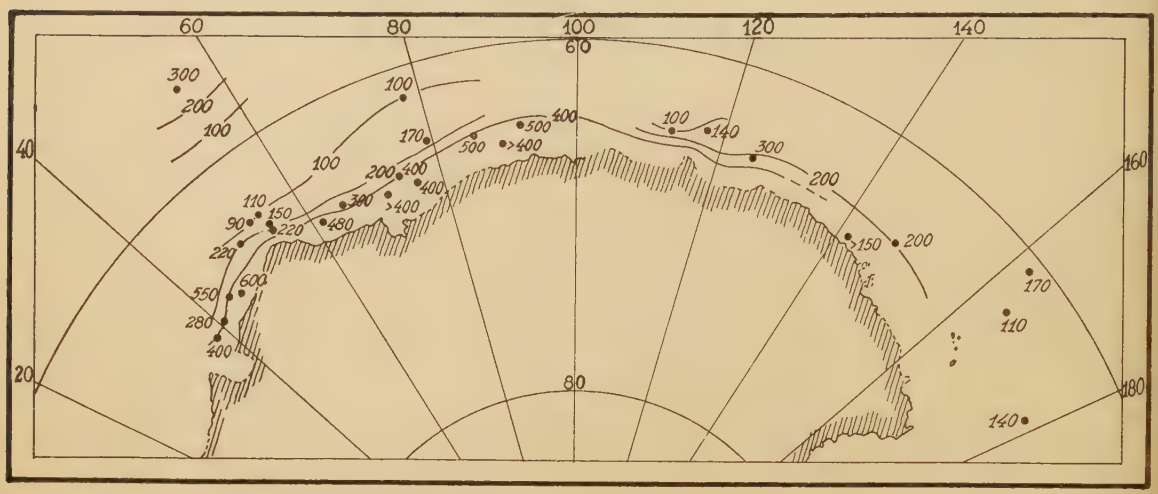


Fig. 11 Thickness in metres of the layer of Antarctic upper water near the Antarctic Continent.

Table V contains the depth of the minimum temperature of the upper water, the observed minimum temperature, and the corresponding salinity at 25 stations which are situated near the continent. If the temperature near the minimum varies a few hundredths of a degree only, the temperature at the lowest depth has been entered. Six of these stations, which are marked by an asterisk, are situated on the continental shelf.

At one of these stations, number 104, the minimum temperature appears to be in error, since it is — 0·13° lower than the freezing temperature which, at atmospheric pressure, corresponds to the observed salinity. It should, however, be observed that the freezing temperature sinks with

TABLE V.

Depth of Minimum Temperature within the Antarctic Upper Water, and Temperature and Salinity at this Depth.

Station No.	Depth of min. temp.	Min. temp.	Salinity.	Station No.	Depth of min. temp.	Min. temp.	Salinity.
	m.	°C.	‰		m.	°C.	‰
22	60	—1·41	33·86	85	80	—1·72	34·30
24	80	—1·44	34·24	86	60	—1·70	34·20
28	150	—1·70	34·32	87	60	—1·73	34·37
30*	150	—1·68	34·39	89*	145	—1·23	34·43
31	150	—1·64	34·40	91	200	—1·74	34·39
33	200	—1·65	34·35	92	60	—1·80	34·25
37	200	—1·61	34·24	95	60	—1·67	34·30
38	300	—1·75	34·27	99	200	—1·82	34·43
40*	200	—1·77	34·24	100*	200	—1·66	34·43
43	100	—1·59	34·20	101	150	—1·81	34·42
44	60	—1·34	34·05	102	100	—1·76	34·35
45	80	—1·42	34·10	104*	247	—2·01	34·45
				107*	145	—1·32	34·37

* Stations on the Continental Shelf.

ncreasing pressure, the decrease being about 0·00074° per metre. Calling the temperature of reezing at atmospheric pressure τ and the corresponding temperature *in situ* τ_s we have at Station 04:

Depth m.	Temp. °C.	Salinity ‰	τ °C.	τ_s °C.	$t-\tau_s$ °C.
99	—1·87	34·45	—1·88	—1·95	0·08
148	—2·03	34·705?	—1·89	—2·00	—0·03
198	—2·04	34·46	—1·88	—2·03	—0·01
247	—2·01	34·45	—1·88	2·06	0·05

The salinity at 148 metres seems doubtful. It is, however, interesting to note that the differences between the observed temperatures and the freezing temperature *in situ* lie close to the limits of the accuracy of the observations. It is physically possible that such temperatures are actually present, if the ice barrier in the region in question reaches to a depth of 150 to 200 metres and at these depths has a temperature which is lower than — 2°. In that case the water which comes in contact with the ice must give off heat until it is cooled to the freezing temperature *in situ*. If it is then carried away, it will retain its low temperature for some time, and the observed temperatures may, therefore, be correct. Thus, it is not justified to discard the values as impossible.

At the stations outside of the shelf the depth of the minimum temperature decreases with increasing distanct from the shelf. Grouping the data according to the depth of the minimum temperature we, therefore, undertake a grouping according to the distance from the shelf. We obtain:

	Number of Stations.	Mean Depth of Min. Temp.	Mean Min. Temp. °C.	Mean Salinity ‰
Stations on the shelf ..	6	181	—1·61	34·38
Depth of min temp. greater than 100 metres ..	8	194	—1·72	34·35
Depth of min. temp. 100 metres or less	11	73	—1·60	34·20

We may consider the water on or near the shelf at the depth of minimum temperature as the water which comes nearest to the winter water. The salinity of the winter water is then 34·38, in excellent agreement with the value S = 34·34, which Mosby (1934), by a different procedure, has found as typical of the winter water in the Weddell Sea.

The temperature of the winter water is less well defined. Mosby introduces the value $t = -1{\cdot}77$, but it seems more correct to adopt the freezing temperature at atmospheric pressure which corresponds to the salinity, $t = -1{\cdot}87°$.

The highest salinity of the winter water is found on the shelf. It is, therefore, of special interest to examine the maximum salinity at the six stations on the shelf. We find:

Station No.	Depth to Bottom m.	Depth of S max. m.	Max. Salinity ‰	Temp. °C.
30	456	400	34·52	—0·97
41	223	200	34·24	—1·77
89	150	145	34·43	—1·23
100	402	378	34·52	—1·33
104	230–275	80	(34·75)	—1·65
107	150–200	193	34·45	—1·19

The value at Station 104 appears doubtful. At this station the observed values at 60, 99, 198, and 247 metres are 33·93, 34·45, 34·46, and 34·45‰ respectively, but at 80 and 148 metres the observations show 34·75 and 34·70‰. If these values were correct the stratification would be very unstable, and this circumstance, in connection with the fact that so low values are not found at any other stations, makes it necessary to discard them. At Stations 30 and 100 the minimum temperature is met with at 150 or 190 metres, where the salinities are 34·38 and 34·43‰ respectively. The increase of both temperature and salinity towards the bottom indicates a slight admixture of deep water, and the maximum salinities, 34·52‰ at both stations, are, therefore, probably not characteristic of the unmixed water on the shelf. The highest salinity of the unmixed water appears, therefore, to be 34·46‰ (at Station 104), and consequently one may assume that generally it not exceeds 34·50‰. This salinity is considerably lower than the maximum salinity of the shelf-water in certain regions of the Weddell Sea, where Brennecke (1921) has observed values as high as 34·68 to 34·70‰. This result has considerable bearing upon the problem of the renewal of the Antarctic bottom water.

The character of the surface water appears to be quite similar to the character of the corresponding water in the Weddell Sea area which Mosby has examined by means of a more extensive material. The lower salinity of the surface layer must be due to the effects of melting in summer and of precipitation, and the higher temperature must be due to heating by radiation, and, to a lesser degree, by convection from the atmosphere.

Near the continent, where areas with more or less open water alternate with areas with close ice, the temperature varies irregularly. This is seen both from the four-hourly observations and from the records by means of the keel thermograph. The latter have not been published since no discussion will be attempted of these rapid variations, which are of a very local nature, and since all major features as to surface temperature can be derived from the four-hourly observations.

So long time was spent in high southerly latitudes (to the south of 65° S.) that it is possible to examine the diurnal variation in a region where the average temperature differs less than 1° from freezing point.

We find:

Surface Temperature in degrees C.

Year.	0^h	4^h	8^h	12^h	16^h	20^h
1929–1930	—1·12	—1·12	—1·13	—1·103	—1·01	—1·07
1930–1931	—0·92	—0·94	—0·87	—0·81	—0·80	—0·85

The observations from 1929–30 comprise the time interval 12th December, 1929, to 25th January, 1930, and the observations from 1930–31, the time interval 13th December, 1930, to 18th February, 1931. The diurnal variation of temperature is similar in both years, the maximum occurs in the early afternoon between 12^h and 16^h, and the minimum at about 4^h. In both seasons the range is about 0·12°.

The average salinities at noon and midnight are:

Salinity in ‰

Year.	at Noon.	at Midnight.	Difference.
1929–1930	33·72	33·65	0·07
1930–1931	33·67	33·66	0·01

The salinity appears to be slightly higher at noon than at midnight, but the difference is very small.

4. THE UPPER WATER OF THE SUB-ANTARCTIC REGION.

Within the upper part of the sub-Antarctic water, between the two convergences, two distinctly different types of water are present, the surface layer of uniform temperature and salinity, and a deeper layer of a salinity which at the southern stations is higher than the salinity of the surface water, and at the northern stations shows a secondary maximum.

Table VI contains the thickness, the temperature and the salinity of the surface layer at 13 stations to the north of the Antarctic Convergence, two of which, stations 74 and 75, are lying north of the sub-Tropical Convergence. It is seen that the thickness varies irregularly, probably because it depends upon the wind velocity and the time during which the wind has been blowing. The surface layer, which is considered here, is, however, not identical with the upper homogeneous layer, since in our cases the temperature often decreases somewhat downwards.

Table VI.

Thickness, Temperature, and Salinity of the Surface Layer at Stations to the North of the Antarctic Convergence.

			Surface layer.		
Station No.	Latitude S.	Longitude E.	Thickness. m.	Temp. °C.	Salinity. ‰
75	36° 41′	114° 55′	30	18·4	35·71
74	37° 59′	110° 59′	30	18·2	35·70
72	40° 18′	104° 31′	60	13·8	34·79
114	41° 09′	148° 48′	60	16·1	35·28
70	42° 35′	96° 46′	60	11·7	34·52
77	44° 05′	147° 35′	80	12·6	35·23
111	44° 11′	143° 36′	60	12·0	34·57
68	45° 10′	87° 13′	100	8·4	34·01
65	47° 43′	76° 48′	40	5·5	33·74
78	48° 24′	146° 29′	100	7·9	34·24
110	49° 00′	114° 13′	75	6·6	33·96
109	51° 26′	101° 34′	60	4·1	33·87
79	52° 14′	152° 46′	30	5·6	33·88

Within the surface layer temperature and salinity increase from south to north. In a T-S diagram (Fig. 12) the values fall nearly on a straight line, including the two values north of the sub-Tropical Convergence. This feature is quite remarkable since external influences, heating, evaporation, and precipitation exercise a great influence upon the surface values.

Below the surface layer we find, as already mentioned, at most stations a layer of maximum salinity within which the value of the salinity decreases towards the south. In a vertical section along a meridian, a tongue of higher salinity must, therefore, be present somewhat below the surface, and in some of the sections which Lotte Möller (1929) has published, using older data, this tongue appears. The temperature and salinity values within this layer are given in Table VII. At the three southerly stations a salinity maximum is lacking, but instead a layer of maximum temperature appears. In the table the data have been added from the depths 200 and 300 metres at Stations 74 and 75 to the north of the Tropical Convergence.

The corresponding values of temperature and salinity are plotted in the T-S diagram in Fig. 12. The points fall near a straight line, although the stations have been taken in widely different longitudes. The line is displaced to the right of the line representing the surface water. The most interesting feature is that the line continues through the points which represent the water at depths of 200 to 300 metres to the north of the convergence. It appears, therefore, probable that the saline water spreads towards the south from a region near the sub-Tropical Convergence,

Table VII.

Depth of Sub-surface Salinity Maximum, and Temperature and Salinity at this Depth at Stations between the Two Convergences. Temperatures and Salinities of Depths of 200 and 300 Metres at Stations 74 and 75 to the North of the Sub-Tropical Convergence.

Station No.	Latitude S.	Longitude E.	Layer of maximum salinity. Depth. m.	Temperature. °C.	Salinity. ‰
72	40° 18′	104° 31′	400	10·2	34·78
70	42° 35′	96° 46′	150	10·8	34·87
77	44° 05′	147° 35′	250	11·6	35·09
111	44° 11′	143° 36′	250	10·2	35·03
68	45° 10′	87° 13′	150	8·2	34·42
65*	47° 43′	76° 48′	350	3·1	34·20
78	48° 24′	146° 29′	400	8·4	34·59
110	49° 00′	114° 13′	150	5·5	34·16
109*	51° 26′	101° 34′	400	2·6	34·22
79	52° 14′	152° 46′	300	4·0	34·14
75	36° 41′	114° 55′	200	12·8	35·24
,,	,,	,,	300	11·6	35·09
74	37° 59′	110° 59′	200	12·8	35·24
,,	,,	,,	300	11·6	35·08

* Temperature maximum but no salinity maximum.

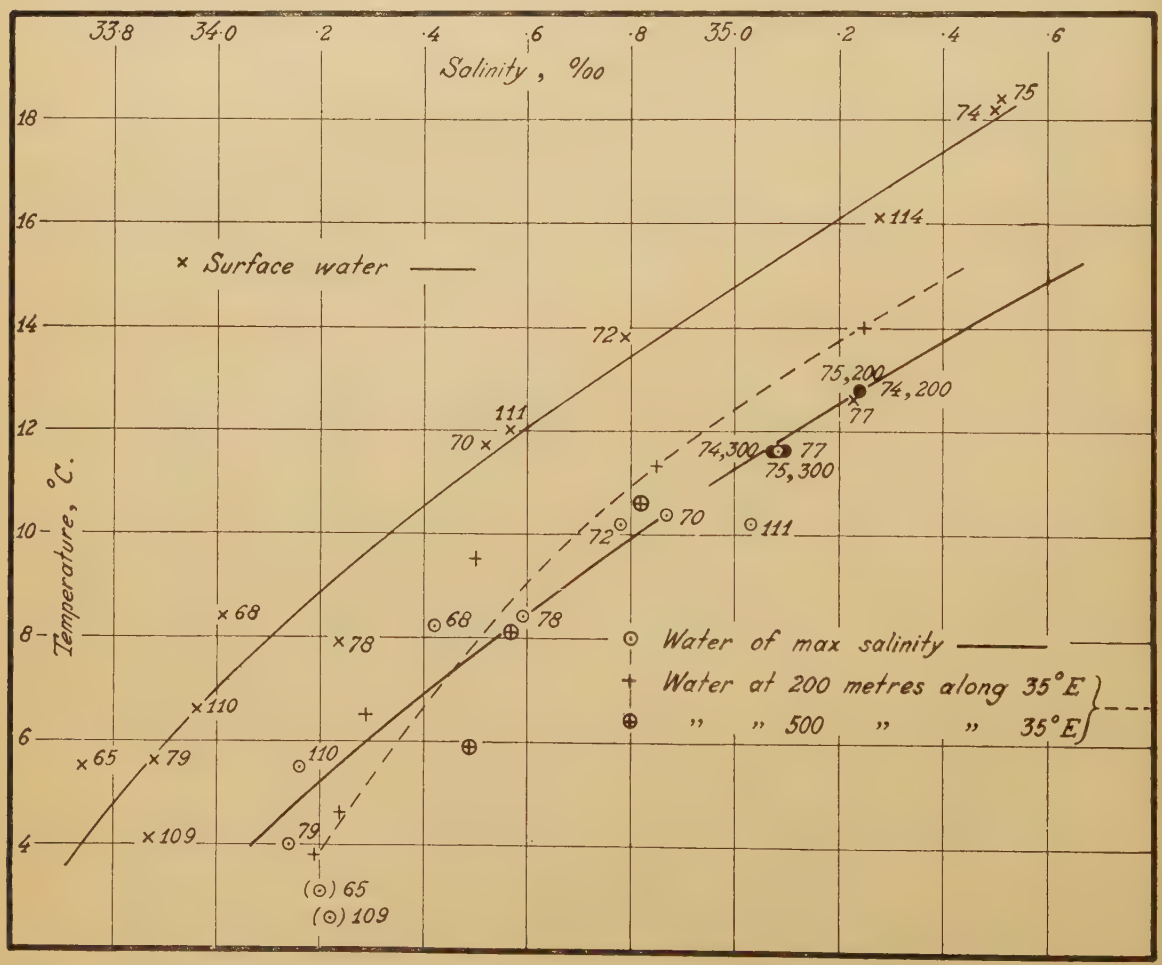


Fig. 12. Temperature and salinity of the surface layer and of the sub-surface layer of maximum salinity to the north of the Antarctic Convergence, and corresponding values at the depths of 200 and 500 metres in the region of the Agulhas current.

and is, in course of time, mixed with colder and less saline surface water, and to a lesser degree with the intermediate water.

This conclusion is, however, not binding, since the general direction of the current is, no doubt, from west to east, and since it is quite possible that the origin of any water mass within the area in question must be sought to the west and not to the north. We can examine this question more closely by means of the charts and sections in the area of the Agulhas current, which recently have been published by Dietrich (1935).

From his charts of the temperature and salinity distribution at 200 and 500 metres we find the following corresponding values of temperature and salinity along the 35th meridian:

	Depth 200 m.		Depth 500 m.	
	Temp.	Salinity	Temp.	Salinity
Lat. S.	°C.	‰	°C.	‰
40°	14·0	35·25	10·6	34·82
41°	11·3	34·82	8·1	34·57
42°	9·5	34·50	5·9	34·49
43°	6·5	34·29		
44°	4·6	34·24		
45°	3·8	34·19		

These values are also entered in the diagram (Fig. 12). It is seen that along the meridian 35° E. the salinity, which corresponds to a temperature higher than about 9°, is less than it is further east, for instance along the meridian 145° E. The eastward increase in salinity between depth of 200 to 500 metres cannot be due to admixture from the surface layer or the deeper layers since these have a lower sailnity. We must conclude that water of higher salinity has been added through a horizontal flow, and this water can only come from the north, from the region of the sub-Tropical Convergence. Thus, it appears very probable that within the sub-Antarctic water a flow towards the south takes place between the depths of 150 to 400 metres. It is, however, also possible that lateral mixing is of importance. As to the movement of the surface layer no conclusions can be drawn.

5. THE ANTARCTIC INTERMEDIATE WATER.

Table VIII contains the depth of the salinity minimum and salinity and temperature at this depth at the stations where the intermediate water undoubtedly was present. The stations have been arranged according to increasing southerly latitude. The last line in the table shows, in degrees of latitude, the approximate distance from the Antarctic Convergence, supposing that the position of the latter has been plotted correctly by Deacon (1934).

TABLE VIII.

Depth of Salinity Minimum, and Temperature and Salinity at this Depth.

Station No.	Latitude N.	Longitude E.	Salinity minimum. Depth. Metres.	Temperature. °C.	Salinity. ‰	Approx. dist. from Antarctic Convergence stated in deg. lat.
75	36° 41′	114° 55′	1200	4·1	34·41	14·1
74	37° 59′	110°·59′	1100	4·8	34·40	13
72	40° 18′	104° 31′	1000	4·6	34·37	11·5
70	42° 35′	96° 46′	1060	4·2	34·37	10·2
111	44° 11′	143° 36′	1150	4·3	34·38	11·4
68	45° 01′	87° 13′	720	3·5	34·25	7·5
78	48° 24′	146° 30′	980	4·4	34·36	7·2

We find that within a great area the intermediate water is of a very uniform character, and between distances of about 10 and 14 degrees of latitude to the north of the Convergence, the salinity is about 34·39 and the temperature about 4·4°. A well-defined change with longitude is not present, but with increasing distance from the Convergence the salinity appears to decrease and the temperature to increase.

It is of interest to compare these few data with the numerous observations from the Atlantic Ocean. Wüst (1935) has examined the T-S relation within the core of the intermediate water in the Atlantic, and has drawn a normal curve which is valid for the entire region of the intermediate water.

By means of this curve he defines:

100% Iw:	$S = 33{\cdot}80‰$	$t = 2{\cdot}2°$	$\sigma_t = 27{\cdot}01$
0% Iw:	$S = 34{\cdot}95‰$	$t = 6{\cdot}6°$	$\sigma_t = 27{\cdot}45$

and by dividing the line which connects the points 100% Iw and 0% Iw in equal parts, he can read off the percentage part of unmixed intermediate water (100‰ Iw) in intermediate water of known temperature and salinity. Wüst's curve is reproduced in Fig. 13, in which the T-S

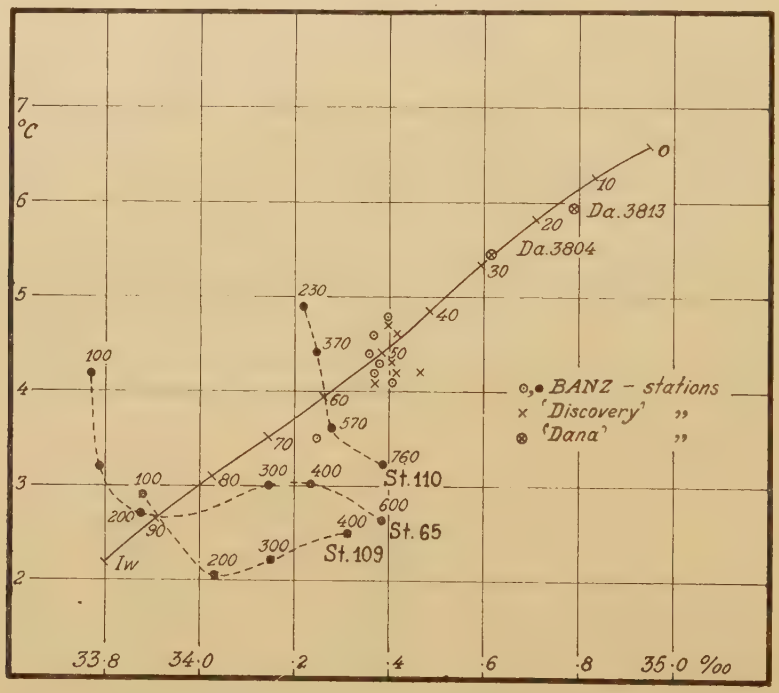


Fig. 13. The T–S relation within the intermediate water of the Atlantic Ocean (according to Wüst) and T–S values of the intermediate water of the Indian Ocean according to observations on R.A.N.Z.A.R.E. stations, "Discovery" stations, and "Dana" stations. T–S curves from stations 65, 109, and 110.

values at the stations in Table VIII are plotted. It is seen that all points fall near the T-S curve from the Atlantic Ocean, and all except one, from Station 68, show that in the region in question the intermediate water contains very nearly 50% of unmixed Antarctic intermediate water according to Wüst's definition.

In Fig. 13 are, furthermore, entered the T-S values at the core of intermediate water according to the observations on the "Discovery II" Stations 427, 428, 431, 432, 433, and 434, lying

between latitudes 42° S. and 36·6° S., on a line running south-east from Port Elisabeth, South Africa. At these stations the core of the intermediate water is met with at depth between 1000 and 1400 metres. Thus, between latitudes 42° S. and 36° S., the intermediate water is found at nearly the same depth over the entire southern part of the Indian Ocean, and from the figure it is, furthermore, seen that from South Africa to Australia, the character of the water is similar.

If Wüst's definition of the unmixed intermediate water is correct, and if his curve is applicable to conditions in the Indian Ocean, we encounter there intermediate water which contains only 50% of the unmixed component already at a latitude of about 42° S., both in longitude 35° E., 90° E., and 146° E. In the last-mentioned longitude this water is present even in latitude 48° S.

In the Atlantic Ocean water of this type is found much further to the north. From Wüst's chart on Pl. XI (1935) we find:

In longitude 10° E., 50% Iw present at 27° S.
„ „ 0 „ „ „ „ 28° S.
„ „ 10° W., „ „ „ „ 28° S.
„ „ 20° W., „ „ „ „ 13° S.
„ „ 30° W., „ „ „ „ 9° S.

The depth of this water is in the Atlantic less than 800 metres. Thus, a considerable difference exists between the intermediate current in the two Oceans, although the character of the water is similar.

The next question which arises in this connection is whether water of the type $S = 33{\cdot}80\%$, $t = 2{\cdot}2°$, which Wüst considers as unmixed intermediate water, occurs at or near the Antarctic Convergence in the Indian Antarctic Ocean. This question can be answered by means of surface observations in the neighbourhood of the Convergence, which was crossed on four occasions. At the first crossing the surface observations were, however, commenced on the southern side of the Convergence, and data which are suited for our purpose are, therefore, available from three crossings only. The surface observations comprise temperature observations at intervals of four hours, and observations of the salinity at noon and midnight. In Fig. 14 temperature, salinity, and σ_t are plotted against the latitude. The curves for salinity and σ_t are smoother than the temperature curves, since they are based on a smaller number of observations. The probable situation of the Convergence is shown in each case. When passing the Convergence, proceeding to the north, we find a more or less pronounced and sharp rise of the temperature and a drop of σ_t, but the salinity remains more or less constant. At the Convergence we have:

Location of Convergence.		Temp.	Salinity
Lat. S.	Long. E.	°C.	‰
53°00′	56°	3·2	33·84
54°45′	88°	2·2	33·81
58°45′	160°	2·1	33·94

Regarding the location of the Convergence, it may be noted that this in all cases appears to lie between one or two degrees of latitude to the south of the position which has been plotted by Deacon (1934). This difference may be accidental or be caused by seasonal shifts. The temperature and salinity correspond very nearly to the values which Wüst considers typical of the unmixed intermediate water in the Atlantic, for which reason we must conclude that, at its place of origin, the intermediate water is of very similar character in the Atlantic and the Indian Antarctic Oceans.

Stations 65, 109, and 110 are situated to the north of the Convergence, but at these stations

no salinity minimum is found. The observed data alone do not indicate the presence of intermediate water, but we can now avail ourselves of Wüst's curve since we have seen that the 100% Iw of the Indian Ocean is identical with the 100% of the Atlantic Ocean. In Fig. 13, showing

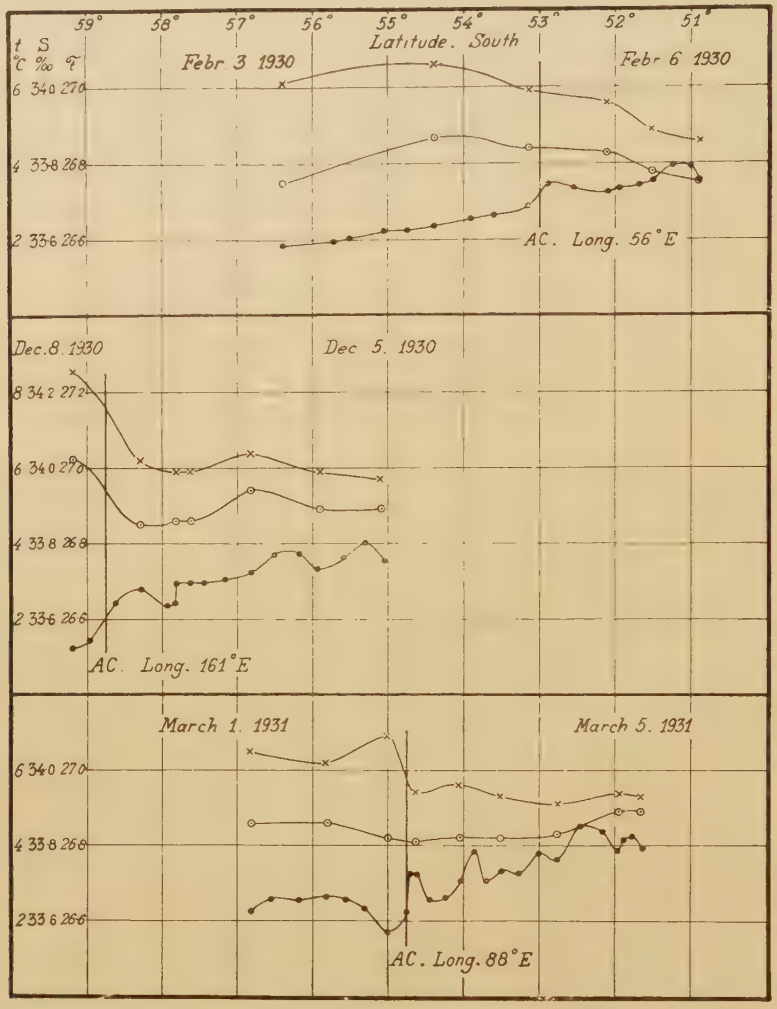


Fig. 14. Surface temperatures (dots), salinities (rings), and densities (crosses) at three crossings of the Antarctic Convergence.

Wüst's curve for the T-S relation at the core of the intermediate water, the T-S curves at Stations 65, 109, and 110 are entered. The latter cross Wüst's curve, and, therefore, at all three stations we meet water of the intermediate type. By means of the graph we find:

			Distance from	Intermediate Water		
Station.	Lat. S.	Long. E.	Convergence.	Depth m.	Temp. °C.	Salinity ‰
65	47·6	76·8	4°	210	2·7	33·92
109	51·5	101·6	2°	120	2·7	33·92
110	49·0	114·2	4°	460	4·0	34·26

Thus, conditions are similar to those in the Atlantic: Near the Convergence the intermediate water sinks rapidly and a rapid mixing takes place.

Still another question is of interest. We have seen that the T-S values of the intermediate water fall near Wüst's curve from the Atlantic, both near the Convergence and at stations which are situated 10 to 15 degrees of latitude to the north of the Convergence. At the last-mentioned stations the water contains about 50% of unmixed Iw, if conditions are similar to those in the Atlantic. This supposition must be examined somewhat more closely. For this purpose observations from the northern part of the Indian Ocean are needed, and use can be made of some data which have been published by H. Thomsen (1935). From his graphs T-S values at the core of the intermediate water have been read off at the "Dana" Station Nos. 3804 and 3813 in about 9° S. 115° E., and 4° S. 100° E., respectively. The values are entered in Fig. 13, from which it is seen that they fall nearly on Wüst's curve. In the eastern part of Indian Ocean Station 3813 is the most northerly station at which the salinity minimum is present. According to Wüst's curve the contents of unmixed Iw is about 15%, and this fact indicates that Wüst's curve applies equally well to conditions in the eastern Indian Ocean as to conditions in the Atlantic. In the western part of the Indian Ocean conditions are more complicated owing to the outflow of Red Sea water, which, in the northern area, spreads under the intermediate water and appears to exert a considerable influence, especially upon the temperature of the intermediate water.

6. THE DEEP WATER.

It was pointed out, that at all stations we encounter one common feature: Below a certain depth, which is great in the sub-Antarctic region, but small in the Antarctic region, an almost homogeneous deep water is present. This feature is, as is well known, characteristic not only of the conditions within the area with which we are now concerned, but of the conditions in the

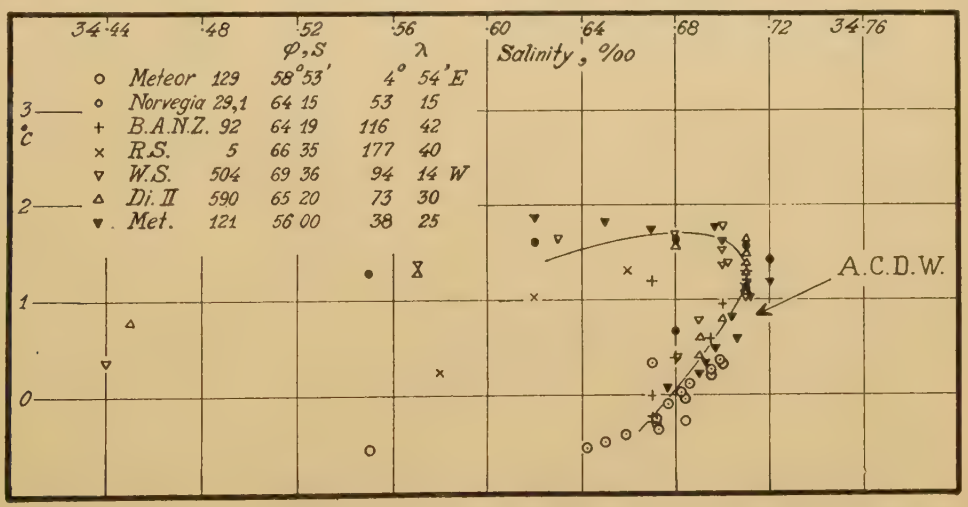


Fig. 15. Temperature and salinity of the deep water at 7 stations around the Antarctic Continent.

Antarctic waters all around the globe. In order to illustrate this fact, data from seven stations which are fairly evenly distributed around the Antarctic Continent are represented in a T-S diagram (Fig. 15). The scale is very open, but, nevertheless, all values fall closely together. It appears, therefore, natural to consider the deep water around the Antarctic continent as water of a special type, and to call it the Antarctic Circumpolar deep water (A.C.D.W.). This water is characterized by temperatures between 0° and 2°, and salinities between 34·68 and 34·74‰.

The deep water for which a special name is proposed has generally been considered as being

composed of two components, Atlantic deep water and Antarctic deep or bottom water. This conception is, no doubt, correct, but the body of water which is formed through these processes is so enormous that it appears appropriate to characterize it by an independent name. The introduction of a separate name has, furthermore, the advantage that regions are more easily pointed

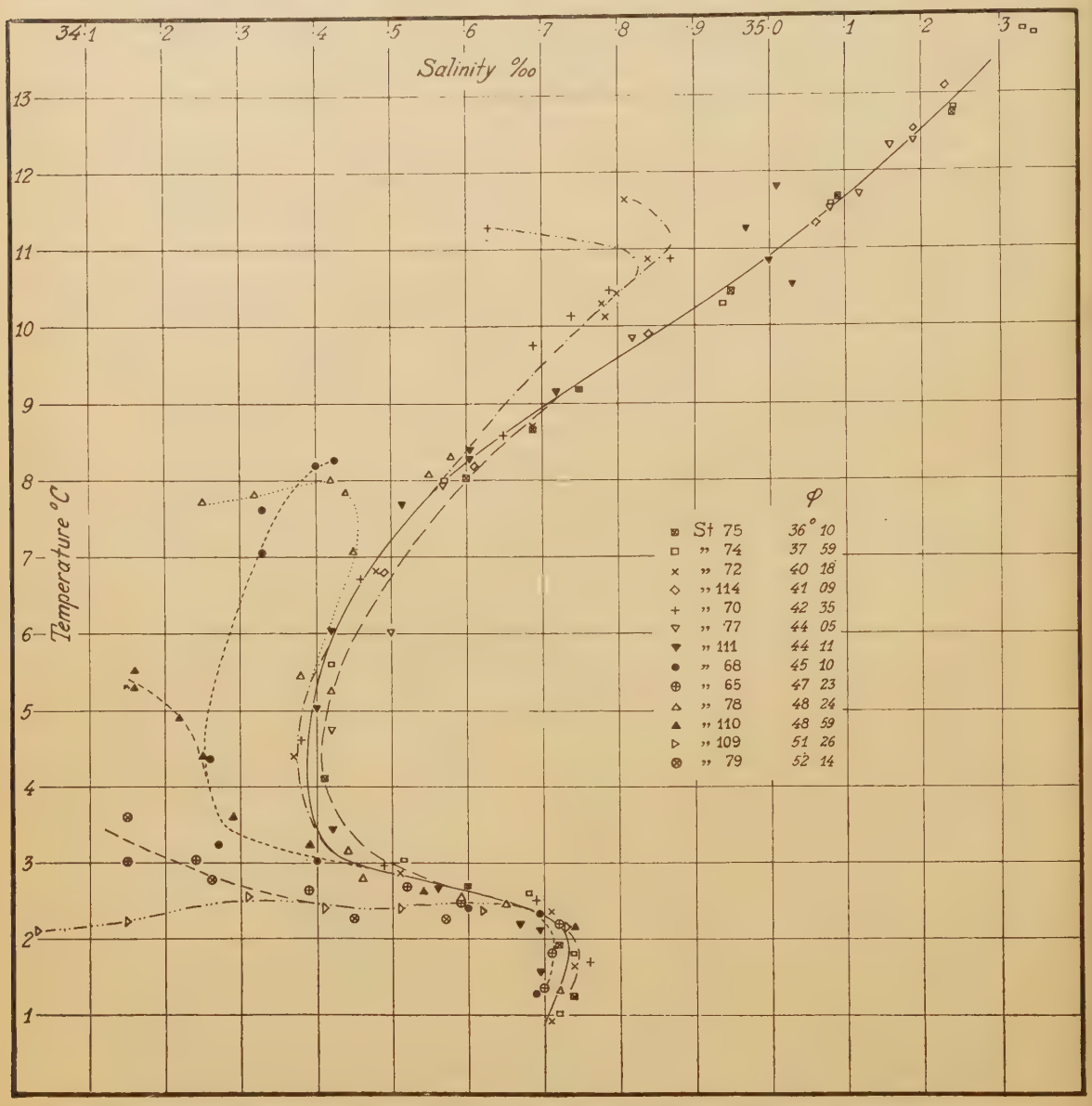


Fig. 16. Temperature and salinity at the B.A.N.Z.A.R.E. stations to the north of the Antarctic Convergence.

out in which either the Atlantic deep water or the Antarctic bottom water exerts an appreciable influence upon the character of the circumpolar water. Returning to Fig. 10 it is for instance seen that at Station Di. 431 a considerable amount of Atlantic deep water is present below 2000 metres, and from Fig. 15 it is seen that at Station "Meteor" 129 the Antarctic bottom water exerts a great influence upon the character of the deepest layers.

The features which are illustrated in Fig. 15 are also shown by means of Figs. 16 and 17. In Fig. 16 all T-S values at B.A.N.Z.A.R.E. stations to the north of the Antarctic Convergence

are plotted. The deep water is of a very uniform character within the entire region. The salinity is perhaps a few hundredths per mille higher at the northern stations, but the existing differences are not much greater than the probable errors of observation. In latitude 40° S. the max. salinity is about 34·74‰ and the corresponding temperature is about 1·9°, but in latitude 46° S. the max. salinity is about 34·715 and the corresponding temperature 1·8°.

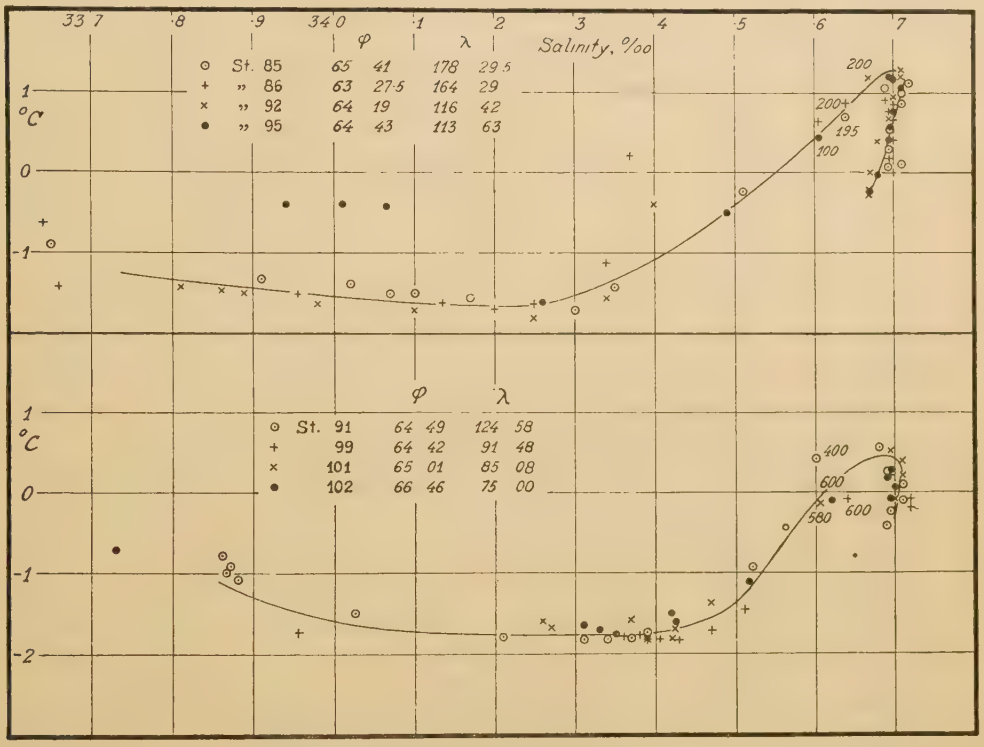


Fig. 17. Temperature and salinity at B.A.N.Z.A.R.E. stations near the Antarctic Continent. Upper part: four stations at some distance from the continental shelf; lower part: four stations very near the shelf.

In Fig. 17 the T-S values from eight stations near the continental shelf are shown. The stations are divided in two groups according to their distance from the shelf. Very close to the shelf (lower part of figure) the upper layer of Antarctic water reaches to a depth of several hundred metres, and the A.C.D.W. is encountered below 700 metres. It has a low temperature, and shows, therefore, considerable admixture of cold water. At a greater distance from the shelf the Antarctic water reaches to about 100 metres only, the A.C.D.W. is found from about 300 metres and downwards, and is warmer. The corresponding values of salinity and temperature at the depth of max. salinity are:

Mean lat. S.	64°33′	65°20′
S‰	34·715	34·705
°C.	1·15	0·25

The difference in latitude is no exact measure of the difference in distance from the rim of the shelf, since the latter does not follow a parallel of latitude, but the compilation shows that near the shelf the general conditions vary rapidly with increasing distance from the continent.

The stations, with which we deal, are situated in the eastern part of the Indian Antarctic

Ocean. It is of great interest to undertake a comparison with conditions in the western Indian Ocean. Wüst (1935) has plotted the characteristic T-S values at the core of the deep current as a function of latitude, and has, south of latitude 35, obtained curves which are quite similar in the Atlantic and western Indian Ocean. He concludes that the deep water of the Indian Ocean is essentially of the same character as that of the deep water of the Atlantic Ocean, and especially that the high salinities in the western Indian Ocean are due to admixture of saline Atlantic deep water.

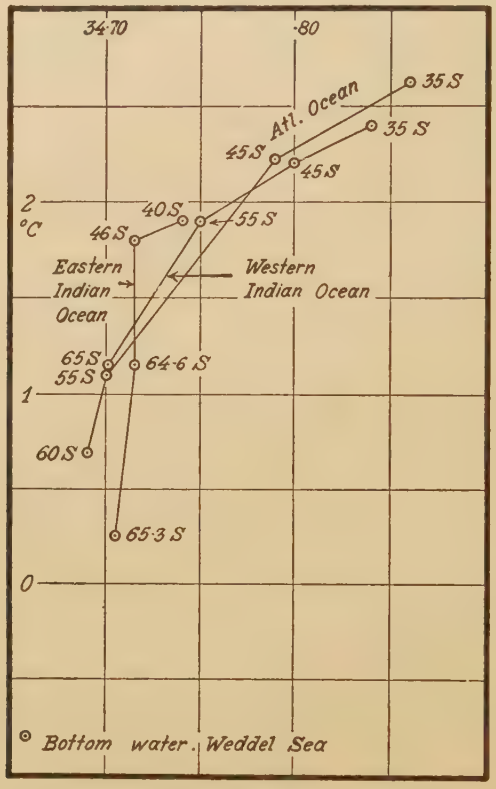


Fig. 18. The T–S relation of the deep water within the Atlantic and western Indian Oceans (according to Wüst) and within the eastern Indian Ocean.

Wüst's curves are reproduced in Fig. 18 and in this figure the above-mentioned data from the eastern part of the Indian Ocean are added. It is seen that the waters are of essentially the same type, but in the eastern region deep water of relatively low temperature and low salinity is evidently present in lower latitudes.

From the region near the Antarctic Continent we have, in the preceding discussion, used only the stations which were worked on the second cruise, 1930–1931. The reason is that in 1929–1930 the salinity values at the southern stations appear to be considerably too low. In order to demonstrate this Fig. 19 has been prepared. We have entered the curve showing the average T-S relation of the deep water according to Fig. 15 the observations from Stations 22 to 44 in 1929–1930, from Stations 99, 100, 101, and 102 in 1930–1931, and from the "Norvegia" Stations 1, 3, and 4, 1929. Stations 99, 100, 101, and 102 lie on the eastern side of the Enderby Land region, in which Stations 22 to 44 are situated, Station 102 being close to Station 28. The "Norvegia" stations lie on the western side, Station 1 being close to Station 44, and Stations 3 and 4

se to Station 37. From the figure it is seen that a considerable difference exists between the tions on the eastern and western side of Enderby Land, the salinities being lower on the west- side. It will be shown, later on, that off Enderby Land we have a region of diverging motion, ce the deep current on the eastern side runs towards the east, but on the western side towards west, and we may, therefore, expect certain difference in the character of the deep water. In

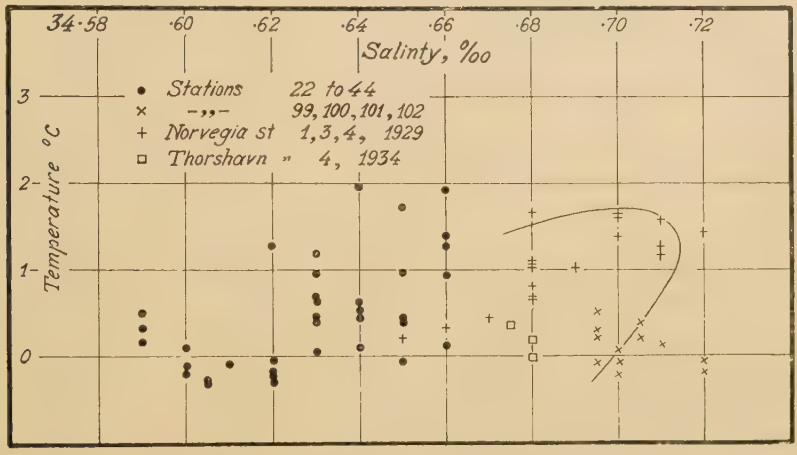


Fig. 19. Temperature and salinity of the deep water in the region of Enderby Land. The curve shows the average T–S relation of the Antarctic circumpolar deep water according to fig. 15.

e central part of the Enderby Land region we should expect salinities between those to the east d the west, but instead we find salinities which, in most cases, are considerably lower than the vest on either side. On the "Thorshavn" expedition in 1933–34 A. Jakhelln took a station in itude 65° 15′ S., long. 49° 46′ E., or very nearly at the centre of the region in which Stations to 44 are situated. With kind permission of Mr. Jakhelln his observations from this station ve been added to Fig. 19. They fall, as should be expected, between the observations from the stern and western areas. In these circumstances we must at present consider the salinities of e deep water at Stations 22 to 44, 1929–1930, as being in error, the values being on an average out 0·05‰ too low. No such objections can be made against the other observations from the me cruise.

7. THE BOTTOM WATER.

The information as to the character of the bottom water is scanty. Only a few stations reach pths greater than 4000 metres, and in 1929–30, when no pressure thermometers were used, the pths of observation are uncertain. In 1930–31, when pressure thermometers were in use, obrvations within a distance of 500 metres from the bottom were obtained at eight stations only.

Table IX contains temperature, potential temperatures, and, in some cases, salinity at the west level of observations at stations where the depth to the bottom was greater than 2000 etres and the deepest observation less than 500 metres above the bottom. The potential temratures have been computed by means of Helland-Hansen's tables (1930). The stations have en divided in two groups: Depth more than 3000 metres or less than 3000 metres, and within ch group the stations are arranged according to increasing southerly latitude. The two seasons 929–30 and 1930–31 have been treated separately, since the data from 1929–30 are less reliable ving to the uncertainty as to the depth of observation. It is seen that the temperature of e bottom water, on the whole, decreases when approaching the Antarctic continent, but the sali-

nity appears to remain nearly constant. The lowest potential temperatures are — 0·54 and — 0·56 at the depths of 4000 and 2635 metres in latitude 64° S.

It is again of interest to undertake a comparison with conditions in the Atlantic. Wüst has shown that the bottom water of the Atlantic Ocean can be considered as a mixture of Antarctic

TABLE IX.

Depth to Bottom, and Temperature and Potential Temperature at Stated Distance of Less than 500 Metres from the Bottom.

Station No.	Latitude S.	Longitude E.	Depth to bottom. Metres.	Distance from bottom. Metres.	Obs. temperature °C.	Potential temperature °C.	Salinity ‰
74	37° 59′	110° 59′	4363	363	1·01	0·65	34·72
72	40° 18′	104° 31′	4050	50	0·92	0·60	·71
70	42° 35′	96° 46′	3336	336	1·70	1·44	·76
68	45° 10′	87° 13′	3260	260	1·28	1·03	·69
46	55° 11′	55° 51′	3950	450	0·14	—0·14	·68
22	61° 44′	77° 57′	3289	289	0·33	0·11	
45	63° 51′	54° 16′	4354	354	—0·22	—0·54	·68
24	64° 44′	79° 00′	3368	368	—0·12	—0·34	
65	47° 43′	76° 48′	2849	349	1·34	1·13	·70
44	64° 55′	54° 35′	2808	308	—0·32	—0·48	
43	65° 27′	54° 35′	2271	271	—0·26	—0·38	
28	66° 05′	73° 50′	2322	322	—0·07	—0·20	
31	66° 11′	65° 10′	2669	169	—0·23	—0·38	
33	66° 30′	61° 08′	2114	114	—0·30	—0·41	
37	66° 33′	45° 32′	2311	311	—0·06	—0·19	
101	65° 01′	85° 08′	3100	284	—0·21	—0·40	·70
87	65° 14′	147° 13′	3072	169	—0·22	—0·41	·70
85	65° 41′	178° 30′	4390	497	0·12	—0·21	·71
84	61° 02′	162° 29′	2806	461	0·62	0·44	·75
86	63° 28′	164° 29′	2896	414	0·00	—0·18	·71
92	64° 19′	116° 42′	2621	219	—0·26	—0·41	·67
91	64° 49′	124° 58′	2635	0?	—0·42	—0·56	·69
99	64° 52′	91° 48′	2466	462	—0·18	—0·32	·72

bottom- or deep-water and Arctic bottom- or deep-water. This feature is especially evident from observation in the western part. Here the bottom water is formed from the components:

North-Atlantic bottom water:

N_I (with admixture of Mediterranean water)

$$t = 2{\cdot}1^\circ, \qquad S = 34{\cdot}92‰$$

Antarctic bottom water:

A_I (mainly as deep water) $\quad t = -0{\cdot}5^\circ$, S = 34·64‰

A_{II} (mainly as bottom water) $\quad t = -0{\cdot}9^\circ$, S = 34·67‰

The T-S curve which is characteristic of the bottom water of the western Atlantic Ocean is shown in Fig. 20, in which the values from the B.A.N.Z.A.R.E. stations are added. In the figure we have, furthermore, entered a point, $t = 2{\cdot}3^\circ$, S = 34·84‰, which characterizes the Atlantic deep water, *AtD*, to the south of South Africa. It is seen that the values in the southern part of the Indian Ocean deviate considerably from those in the Atlantic, but they fall between the point *AtD* and A_{II}, indicating that the bottom water is composed of Atlantic deep water and Antarctic bottom water. The bottom water is, therefore, of essentially the same type as the Antarctic Circumpolar deep water, but near the continent the presence of Antarctic bottom water is more conspicuous than is the case in other localities.

It lies close at hand to assume that a renewal of the bottom water takes place all along the elf since the water on the shelf is cooled effectively, and simultaneously the salinity of the ater is increased due to processes of freezing. Temperature sections alone appear to support is view.

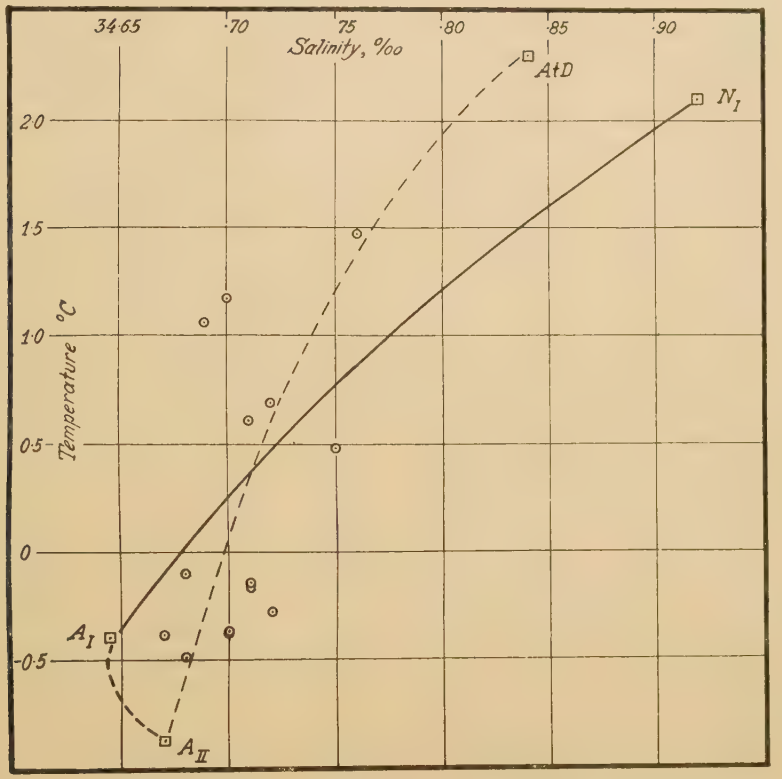


Fig. 20. T–S relation of Atlantic bottom water, according to Wüst, and temperature-salinity values of the bottom water of the Indian-Australian Antarctic Ocean.

Fig. 21 shows three temperature sections at right angles to the continent. In each section the ccumulation on and near the shelf of cold water of temperature below $-1{\cdot}5^\circ$ is seen, and at ome distance from the shelf the much warmer deep water dominates. Furthermore, the presence f cold bottom water close to the continent is clearly recognized. This cold water, with tempera- ures below zero degree, rises abruptly along the continental slope, and it seems, therefore, natu- al to assume that it is renewed by cold water sinking down from the shelf. Such a process ppears, however, improbable in view of the fact that the maximum salinity on the shelf was ss than 34·5‰, whereas the salinity of the bottom water is about 34·68‰. Water of a suffi- ently high density may be formed occasionally, as shown by some of the observations on board Thorshavn", which will be published and discussed by A. Jakhelln, but the present data strongly ndicate that this process is not an ordinary one. On the whole the renewal of the bottom water annot take place regularly along the shelf. The temperature and salinity values indicate that he bottom water flows towards the east, coming from the Weddell Sea area, and that addition f cold and less saline upper water only takes place intermittently.

It is possible that the bottom water, which is formed in the Ross Sea, and which according to he observations on board "C. A. Larsen" ("Discovery" Reports, 1930) reaches salinities up to 4·80‰, contributes to the renewal of the Antarctic bottom water, but, within the region dealt

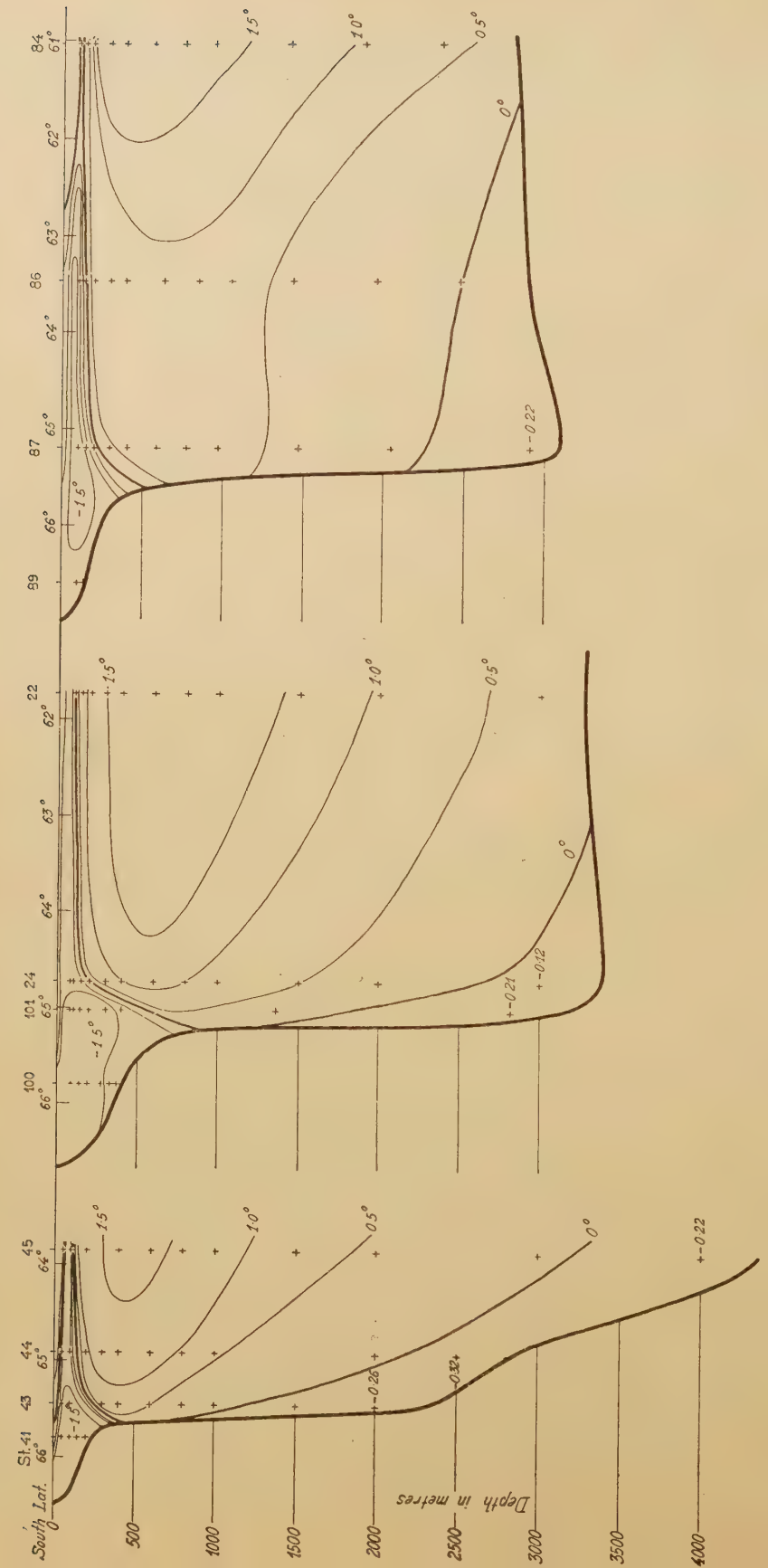


Fig. 21. Temperature sections at right angles to the Antarctic Continent.

with here, no evidence of an admixture of such water appears. It is possible that Ross Sea bottom water plays a part further to the east, but this question cannot be discussed here.

On a previous occasion (1931) the author has advanced the hypothesis that the Antarctic bottom water is formed all along the continent, flows towards the west, and enters the Atlantic Ocean, since the bottom configurations between South America and the Antarctic continent prevents free circulation around the continent. This view can no longer be upheld. The origin of the greater part of the Antarctic bottom water is, no doubt, in the Weddell Sea, from which area the water spreads towards the north and the east.

8. OXYGEN.

The observations of the oxygen contents support the view that both the bottom and deep water flows towards the east along the continent. Oxygen observations are available from 11 stations, all of which are situated to the south of latitude 63° except Station 46, which lies in 55° 11′.

In the upper layers we find, at all stations, high oxygen contents. The variations from one

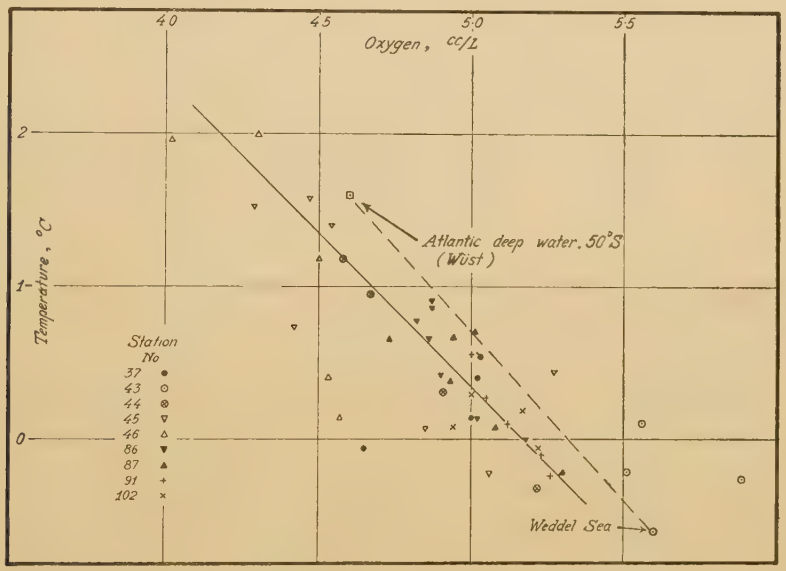


Fig. 22. Temperature and oxygen values of the deep water near the Antarctic Continent according to B.A.N.Z.A.R.E. observations.

locality to another are irregular, and of no special interest, but in the deep water and the bottom water we encounter conditions which show some very interesting features. There low oxygen contents are, as a rule, associated with a high temperature, and vice versa.

In order to illustrate this feature the corresponding temperature and oxygen values have been entered in a T-O_2 diagram (Fig. 22). The values show a considerable scattering, but group themselves, nevertheless, around the straight line which has been drawn. In the figure we have, furthermore, added the points

$$t = 1{\cdot}6^\circ \qquad O_2 = 4{\cdot}6 \text{ c.c./L}$$

and $$t = -0{\cdot}6^\circ \qquad O_2 = 5{\cdot}6 \text{ c.c./L}$$

which, according to Wüst, characterize the "mittlere" Atlantic deep water and the Weddell Sea bottom water respectively. The straight line in the figure runs nearly parallel to a line between these two points, but is displaced somewhat towards lower oxygen values, indicating that the water masses in question represent mixtures of these two types of water which have lost some

oxygen. The low oxygen contents of the Atlantic water show that a long time has passed since this water left the upper layer, whereas the Weddell Sea water more recently was mixed with surface water.

At Station 43, which is situated very near the slope of the continental shelf, the oxygen contents of the deep water and the bottom water are remarkably high. The high oxygen contents indicate that admixture of water from the shelf has recently taken place. The very low temperatures at this station support this view, and here we find, therefore, evidence that a renewal of the bottom water may occasionally take place in the region of Enderby Land, where this station lies.

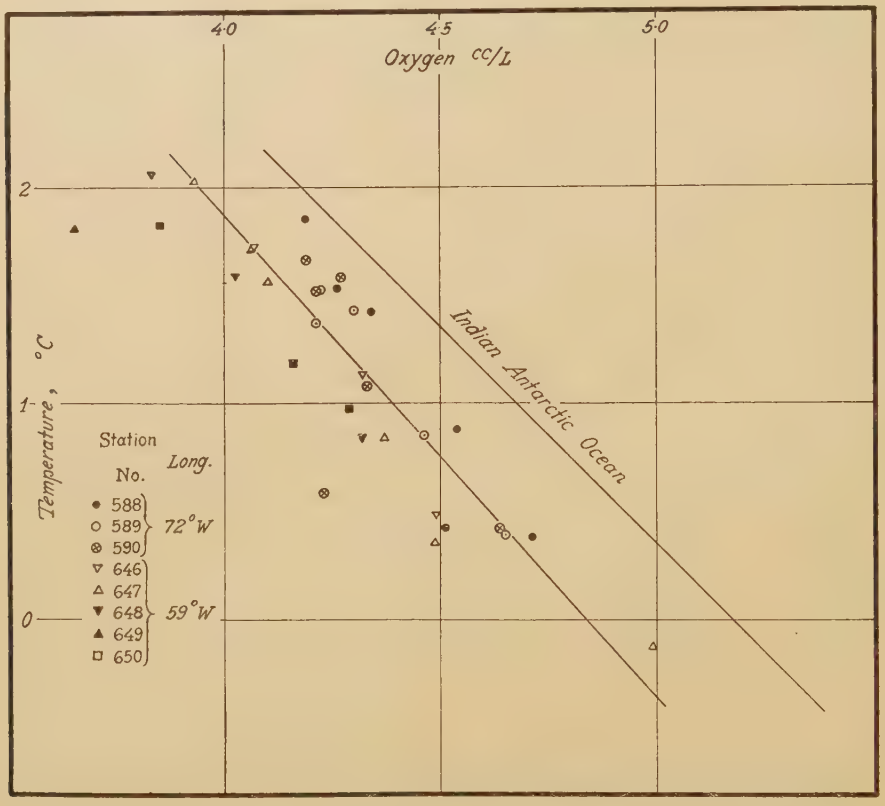


Fig. 23. Temperature and oxygen values of the deep water in the Drake passage according to "Discovery" observations.

Evidence of a corresponding renewal is not found at any of the stations further to the east. To the contrary, at these stations the oxygen contents are generally lower than the contents in the Weddell Sea water of the same temperature, as should be expected if the water flows from the Weddell Sea area, and if only small quantities of surface water have been added in course of time. In these circumstances the consumption of oxygen owing to processes of oxydation and perhaps to the respiration of organisms, is greater than the addition of oxygen by admixture of upper water.

It is of interest to undertake a similar study of the waters in Drake Passage. The observations on board "Discovery II" in 1931 give some very interesting results. In Fig. 23 the single corresponding values of temperature and oxygen at eight "Discovery" stations are plotted, all from deep water of salinity higher than 34·65. Stations 588 to 590 are situated in about longitude 72° W., and between latitudes 66° S. and 65° S., and Stations 646 to 650 are situated in about

longitude 59° W. and between latitudes 60° S. and 56° S. It is seen that the values from Drake Passage group themselves very well around a straight line which is nearly parallel to the line from the Indian Antarctic Ocean, but displaced somewhat towards lower oxygen values. From these data the deep water in the Drake Passage appears to be "older" than the corresponding water in the Indian Antarctic Ocean, but it must be admitted that other observations from the Drake Passage give results which deviate very much from these. It may be added that further to the east, in the South Shetland Sea, the deep water shows higher oxygen contents, probably owing to admixture of the Weddell Sea bottom water of high oxygen contents.

Mr. A. Jakhelln has kindly permitted me to examine his observations on board the "Thorshavn" in 1933–34. The "Thorshavn" stations were taken near the continental shelf between longitudes 49° 46′ E., and 112° 28′ W. The greater number of the stations are situated in the region of the B.A.N.Z.A.R.E. stations, and a few to the west of this region. The average longitudes are:

B.A.N.Z.A.R.E. stations		86° E.
"Thorshavn"	„	105° E.
"Discovery"	„	64° W.

In Fig. 24 the "Thorshavn" temperature and oxygen values below the level of maximum temperature are plotted. At one station the oxygen values are remarkably high, indicating local

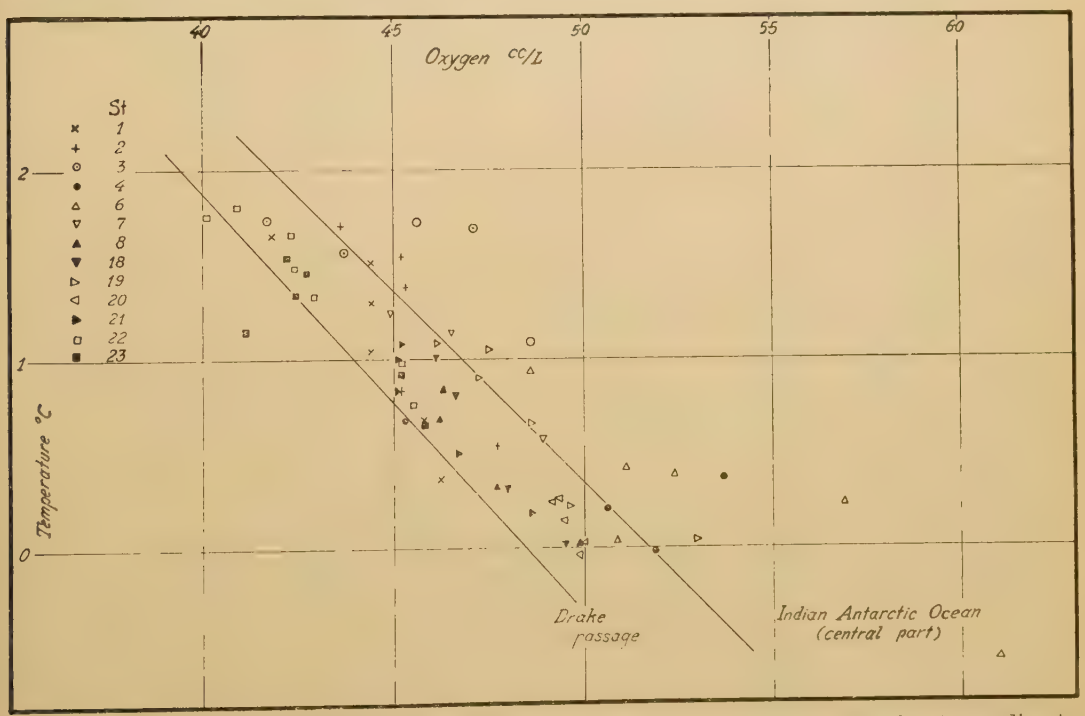


Fig. 24. Temperature and oxygen values of the deep water near the Antarctic Continent according to "Thorshavn" observations.

renewal of the deep water, but otherwise most of the points fall between the two previously determined lines. A line, showing the average relation, would fall nearest to the line which is characteristic of the central part of the Indian Antarctic Ocean, as should be expected. It is especially noteworthy that the values from the two most easterly stations, Station 22 and 23, fall nearest to the line which characterizes conditions in the Drake passage. These data, therefore, strongly confirm the conclusion that both the deep water and the bottom water flow towards the

east around the Antarctic continent, and that the greater part of the bottom water is formed in the Weddell Sea area.

9. VERTICAL SECTIONS.

In the preceding discussion we have made use of a few vertical sections showing the temperature distribution in the vicinity of the Antarctic Continent. The stations have not been taken with the construction of more extended vertical sections in view, but it is, nevertheless, possible to construct one complete section from the Antarctic Continent to Tasmania. The figures, showing the distribution of the various elements, obtain, however, a schematic character owing to the great distance between the stations. We avail ourselves of the observations at Stations 87, 86, 84, 79, 78, and 111.

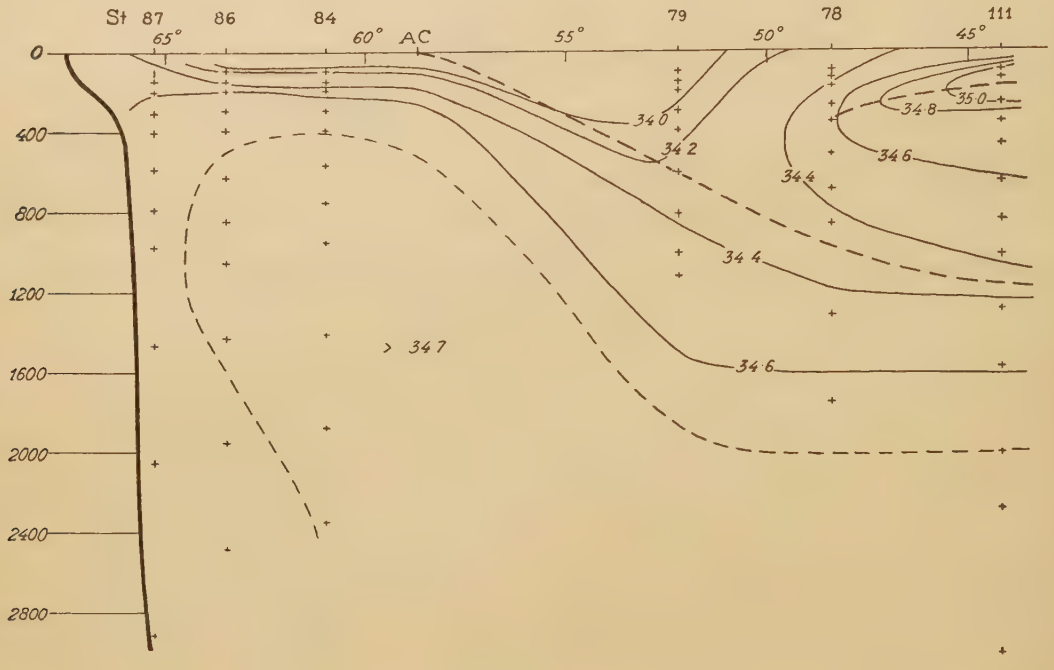


Fig. 25. The salinity in a vertical section between the Antarctic Continent and Tasmania.

Salinity. Fig. 25 shows the vertical distribution of salinity. To the south of the Antarctic Convergence, which, according to the surface observations, is situated in 58° 45′ S., we find a thin upper layer of low salinity, which has its greatest thickness near the Continent, but in this particular section the increase in thickness towards the shelf is less than in most other regions. From a depth of about 400 metres and downwards we find water of very uniform salinity, which is slightly higher than 34·70‰. This water is the Antarctic circumpolar deep water, which in high southerly latitudes approaches the surface.

To the north of the Convergence the depth to this deep water sinks rapidly from about 500 metres at the Convergence to about 2000 metres in latitude 51° south. The slope of the upper boundary, which in the figure appears to be quite steep, is, however, only about 1 : 580. To the north of 51° S. the upper boundary of the deep water appears to run horizontally. In this region the salinity minimum which characterizes the intermediate Antarctic water is clearly seen. The core of the intermediate water sinks from the surface at the Convergence to a depth of nearly 1200 metres in 44° S., the maximum slope being about 1 : 1000. Within the upper water, between

latitudes 44° S. and 50° S., the tongue of maximum salinity is conspicuous. The axes of this tongue and of the intermediate water are indicated.

Temperature. The vertical distribution of temperature is shown in Fig. 26. Attention is drawn to two features only: (1) the uniform temperature of the deep water, and (2) the indication of a high temperature of the saline water to the north of 50° S. The temperature distribution in the immediate vicinity of the shelf has already been discussed.

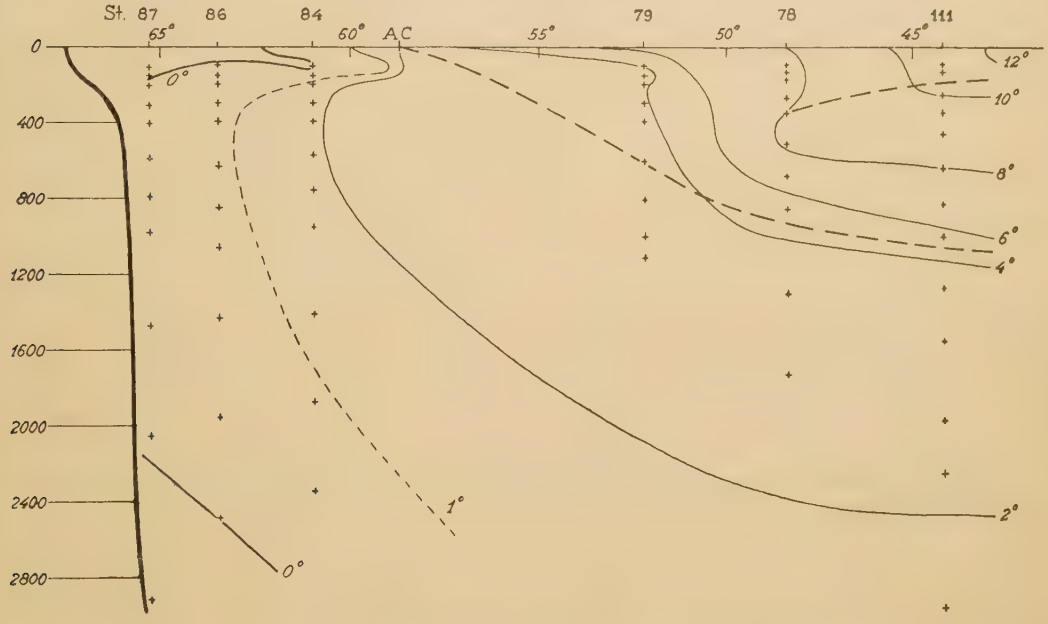


Fig. 26. The temperature in a vertical section between the Antarctic Continent and Tasmania.

Specific Volume Anomaly. In Fig. 27 the distribution of the anomaly of the specific volume is shown. Within the deep water the anomaly increases very slowly when proceeding to the north from the continent, but to the north of the Convergence a rapid increase takes place in the layers above the deep water, especially between the Convergence and latitude 48° S. The importance of this distribution to the possible character of the currents will be discussed later on. Here it is sufficient to mention that the anomaly is nearly constant both within the intermediate water and within the tongue of saline water to the north of 50° S.

Stability. At the stations between the Antarctic continent and Tasmania the stability below 80 metres has been computed by means of Hesselberg and Sverdrup's tables (1915). Above 80 metres the stability is, as a rule, small. The results of the computation are shown in the section, Fig. 28. The stability is, on the whole, small within the entire region, and is especially small in the deep water, where it decreases towards the continent. Within the deep water the values are similar to those which v. Schubert (1935) has derived from the "Meteor" observation in the Atlantic Antarctic Ocean.

Two regions with great stability occur. In an interval of depth from about 100 or 200 to nearly 400 metres a maximum of stability is present at all stations except the most southerly, and directly above the Antarctic intermediate water the stability is very great, surpassing 200 at a depth of 1000 metres at the most northern station.

In two regions the stability is negative. One is situated near the continent, the other in the most northern part of the section. The first region with instability is found at the transition

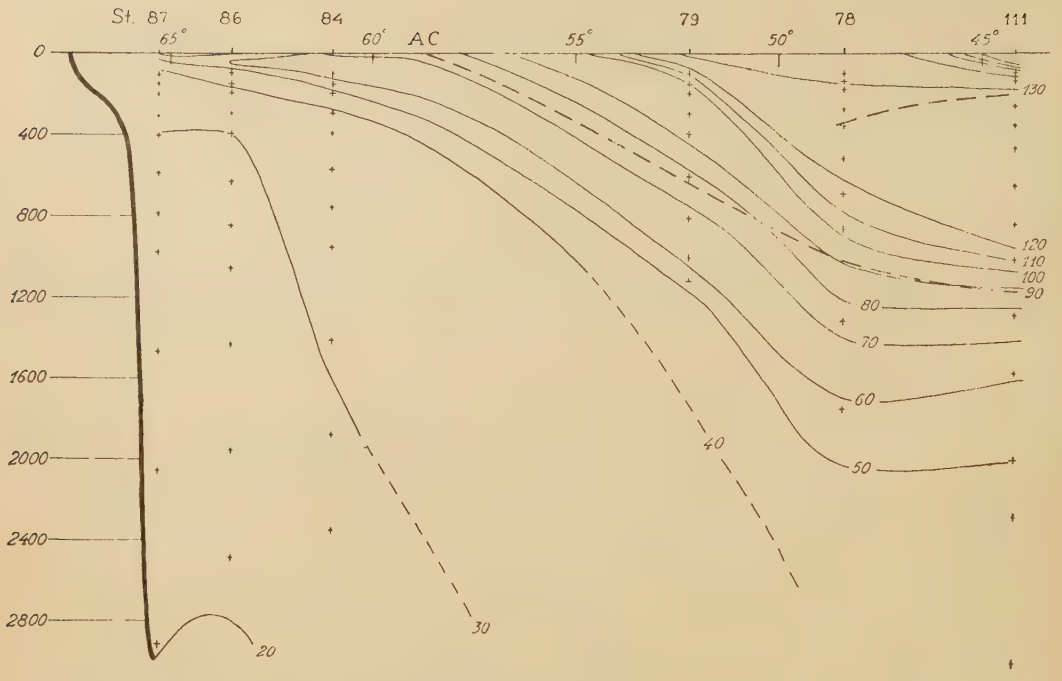


Fig. 27. The anomaly of the specific volume ($10^5 \Delta \alpha$) in a vertical section between the Antarctic Continent and Tasmania.

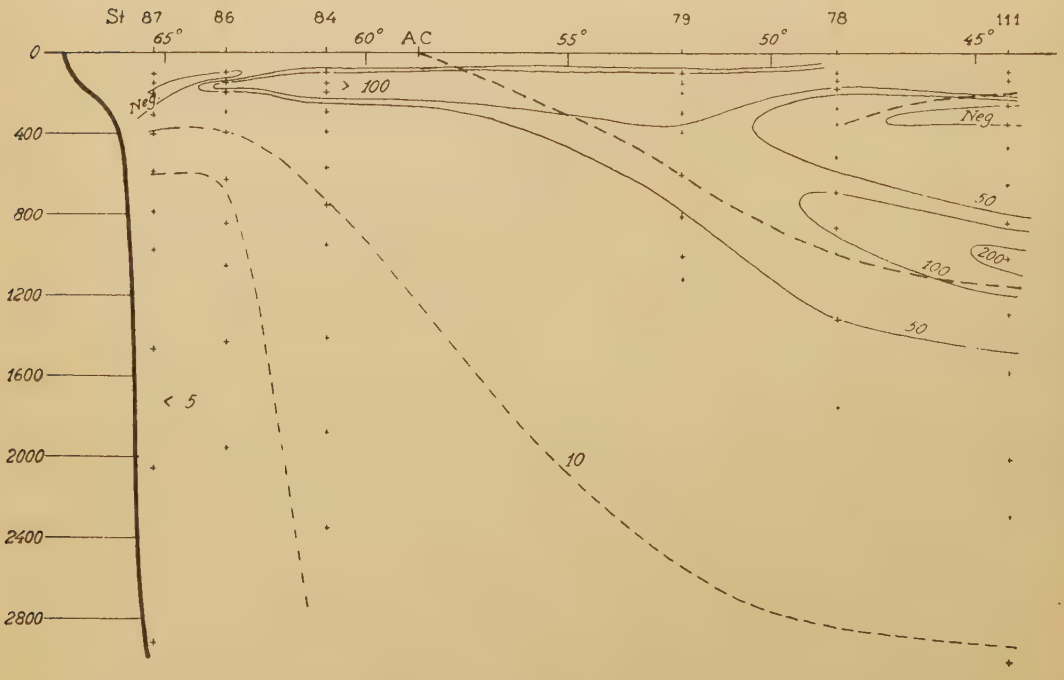


Fig. 28. The stability (10^8E) in a vertical section between the Antarctic Continent and Tasmania.

between the cold Antarctic upper water and the warmer deep water, and at depths at which the temperature increases rapidly downwards. Within this boundary layer the stability is small or negative all along the Antarctic Continent, as evident from the variation of σ_t. The second region is situated within the warm and saline sub-surface flow in the upper layers, and slightly below the axis of maximum salinity. Within both regions rapid mixing probably takes place.

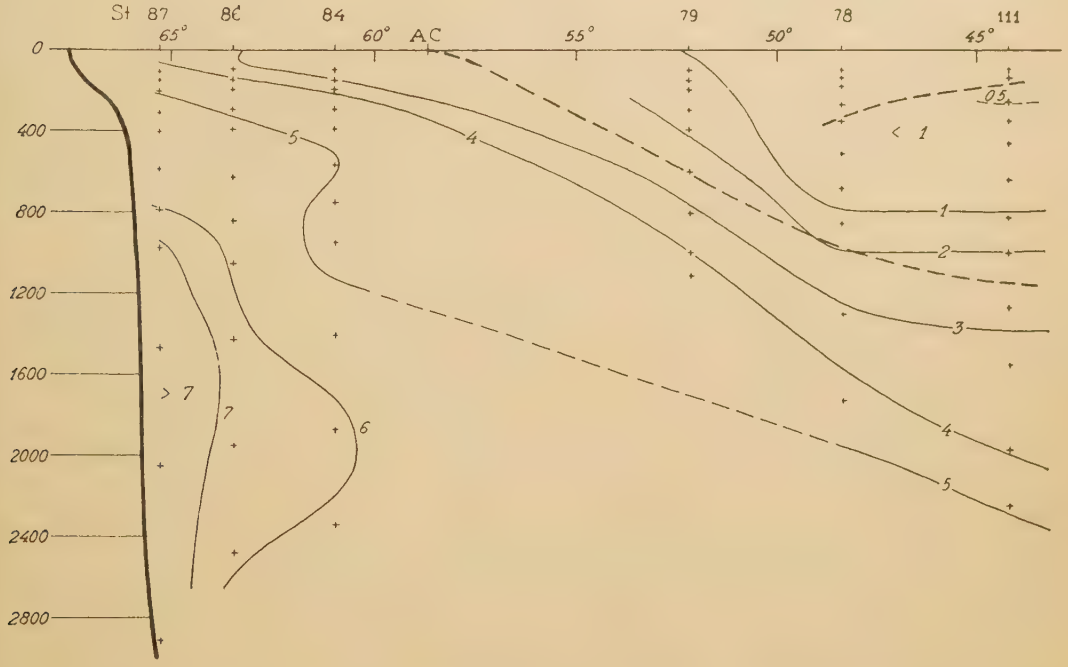


Fig. 29. The silicate (in mg/L) in a vertical section between the Antarctic Continent and Tasmania.

Silicate. The vertical distribution of silicate, as shown in Fig. 30, exhibits some interesting features. At the surface the contents of silicate are much higher to the south of the convergence than to the north. The deep water shows, on the whole, a high concentration of silicate, which increases slowly with depth and remarkably rapidly towards the continent. This increase towards the continent is based upon observations from three stations and must, therefore, be considered as a real feature and not as a result of accidental errors of observations.

In order to offer an explanation of these features it is necessary to say a few words about the conditions which govern the contents of silicate in the sea water. In the upper layers, where plankton production takes place, silicates are used by numerous organisms for building up their crusts. When these organisms die, their crusts sink and are gradually dissolved in the water. Thus, silicates are brought back to the sea water by dissolution of such crusts, but the contents may also increase owing to transport from layers which are rich in silicate, either through the direct action of horizontal or ascending currents or through the action of the eddy convectivity. Under stationary conditions when the silicate contents in a given locality remain constant, the amounts which are lost owing to the growth of organisms and (or) processes of transportation balances the amounts which are added by dissolution of dead organisms and (or) processes of transportation.

Conditions which favour an accumulation of silicates are evidently present in regions where an ascending motion of the deep water exists, since this counteracts the sinking of dead organisms.

and since the deep water which flows towards such a region is rich in silicates. The accumulation of silicates along the slope of the continental shelf, therefore, indicates the existence of an ascending movement near the slope. The fact, that near the shelf the stability is very small, supports the view that an upwards movement takes place.

The presence of such an ascending movement would account for the high silicate values in the upper layers of the Antarctic water, which probably is an important factor to the development of organisms in this water.

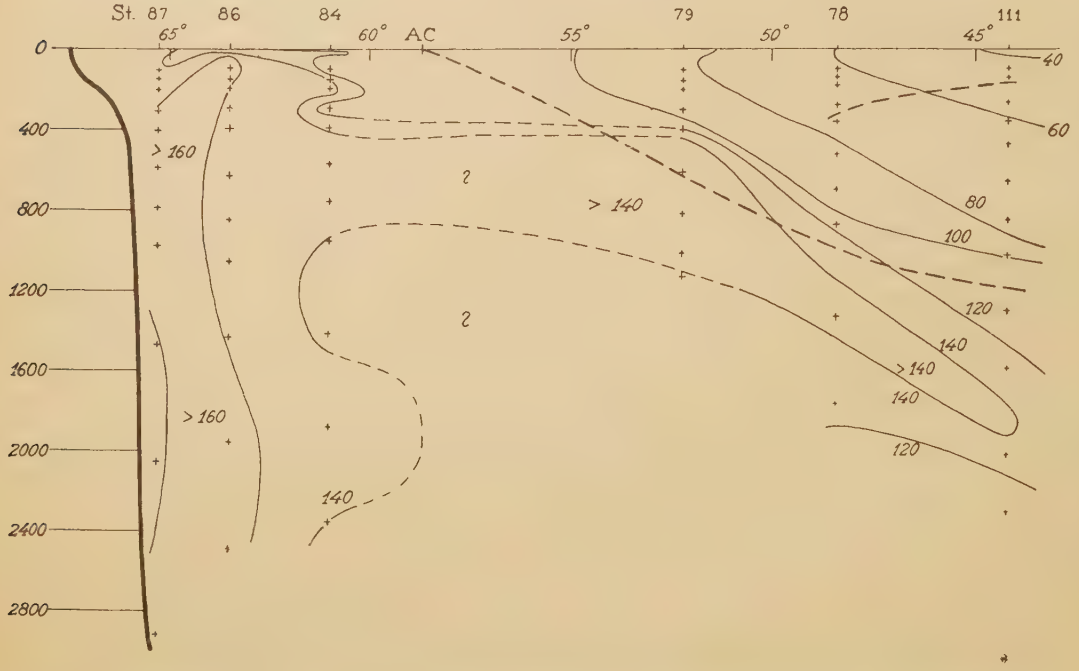


Fig. 30. The phosphate (in mg/L) in a vertical section between the Antarctic Continent and Tasmania.

To the north of the convergence the concentration of silicate is between 2 and 3 mg./L. within the intermediate water, but it decreases upwards, and is to the north of 50° S. less than 1 mg./L. in the upper 800 metres. In this region both the surface layer and the sub-surface layer of high salinity contains very small amounts of silicate. The latter feature shows clearly that the water of the saline sub-surface layer belongs typically to the tropospheric system.

Phosphate. The vertical distribution of phosphate shows several similar features (Fig. 30). In the sea water the phosphate cyclus is similar to the silicate cyclus, but since phosphates are more rapidly dissolved, high phosphate concentrations are found nearer to the surface. The increase of the phosphate contents towards the continent, and the high values which, off the continent, are found nearly to the surface, indicate again an upwards vertical movement near the continental slope, which would account for the high phosphate values within the Antarctic upper water.

To the north of the convergence the phosphate contents are about 120 mg./L. within the intermediate water, but above this the contents decrease rapidly when approaching the surface, as was the case with the contents of silicate. Within the deep water a secondary maximum of phosphate is present in the northern region, but an explanation of this feature cannot be offered.

A few similar vertical sections can be constructed by means of the observations at Stations

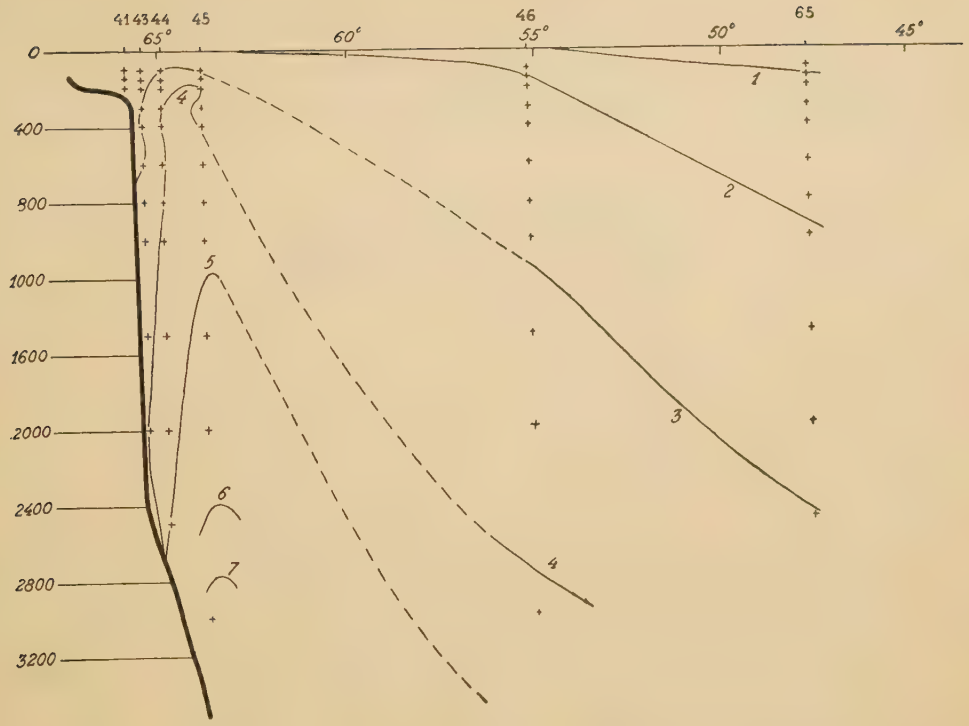


Fig. 31. The silicate (in mg/L) in a vertical, south-north section in longitude 55° E.

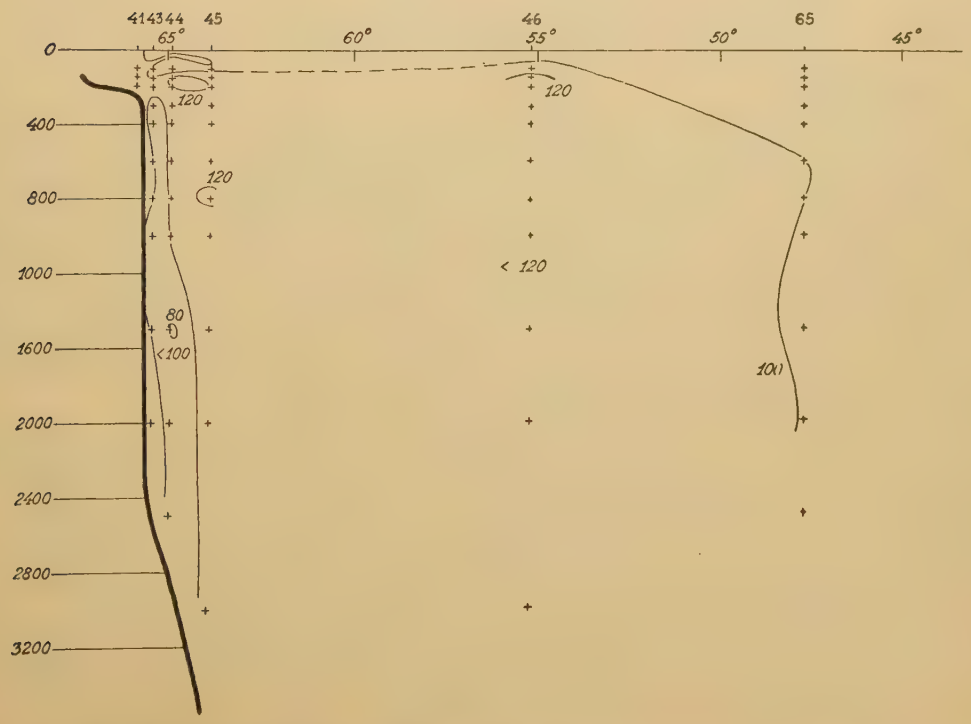


Fig. 32. The phosphate (in mg/L) in a vertical, south-north section in longitude 55° E.

41, 43, 44, 45, 46, and 65, but for this purpose these stations are still less favourably spaced. At several of these stations the salinity values appear doubtful, and salinity, spec. volume anomaly, and stability have, therefore, not been represented. The temperature is of no special interest, and we shall only consider silicate and phosphate and, in addition, oxygen.

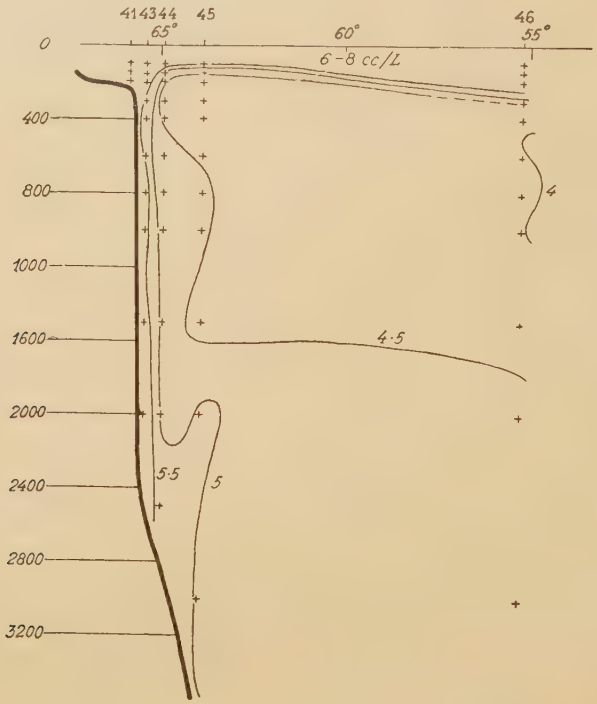


Fig. 33. The oxygen (in ml/L) in a vertical, south-north section in longitude 55° E.

The distribution of these elements does not show such systematic features in this section. The contents of silicate (Fig. 31) are highest at some distance from the continental slope. The phosphate contents (Fig. 32) show small variations with a minimum near the continental slope. whereas the oxygen contents (Fig. 33) are at a maximum along the slope.

These distributions may indicate a descending motion along the slope and an ascending motion at some greater distance, or perhaps they show that the ascending motion near the slope temporarily has been replaced by a descending one, owing to formation of especially heavy water on the shelf. That such processes take place are, as already mentioned (p. 107), clearly seen from some of the observations on the "Thorshavn" expedition.

The features which characterize the eastern section, Antarctic Continent–Tasmania, appear to be present within the entire region to the east of the Kerguelen Ridge. At the stations near the continent the silicate values are considerably higher than at the northern stations, and it is especially characteristic that near the continent the highest phosphate values, as a rule, are found above 300 metres, whereas at the northern stations the maximum values are met with at great depths. It seems difficult to explain the accumulation of silicate and the high phosphate contents of the upper layers near the continental slope without assuming an ascending motion. The present observations indicate, therefore, such a motion, but further evidence is very desirable.

In the preceding discussion we have not used the pH values since these show very small variations.

10. RESULTS OF DYNAMICAL CALCULATION.

In Table III the anomaly of the specific volume $10^5\ \Delta a = 10^5\ (a - a_{35,0,0})$ has been added in all cases in which the salinity has been considered trustworthy. By means of these values the anomaly of the geopotential of standard isobaric surfaces is easily computed:

$$\Delta D = \int_o^p \Delta a dp$$

where ΔD is the anomaly of the geopotential in "dynamic metres", and p the pressure in decibar.

The results of the computation are presented in Table X.

TABLE X.

Anomalies of Dynamic Depth (in Dyn. Metres) of Standard Isobaric Surfaces.

ssure ibar	45	46	65	68	70	72	74	75	77	78	79	84	85	86
100	0·080	0·098	0·137	0·150	0·172	0·177	0·188	0·190	0·139	0·134	0·128	0·067	0·064	0·072
200	0·123	0·179	0·253	0·286	0·316	0·319	0·346	0·347	0·279	0·262	0·246	0·120	0·100	0·116
300	0·158	0·242	0·348	0·416	0·454	0·456	0·489	0·490	0·414	0·386	0·350	0·162	0·131	0·150
400	0·193	0·295	0·431	0·542	0·592	0·595	0·622	0·624	0·544	0·507	0·447	0·199	0·161	0·182
500	0·260	0·392	0·579	0·758	0·854	0·858	0·879	0·882	0·790	0·751	0·619	0·268	0·220	0·240
600	0·323	0·487	0·705	0·936	1·092	1·095	1·130	1·133	1·025	0·982	0·764	0·334	0·280	0·296
000	0·383	0·575	0·817	1·094	1·299	1·300	1·357	1·367	1·219	1·181	0·895	0·399	0·339	0·354
500	0·523	0·775	1·057	1·414	1·709	1·700	1·787	1·810		1·566		0·554	0·477	0·491
000	0·658	0·953	1·270	1·671	2·014	1·993	2·092	2·110		1·856		0·699	0·612	0·620
000	0·918	1·248		2·111	2·474	2·433	2·577	2·595				(0·954)	0·867	(0·848)

TABLE X (continued).

87	89	91	92	95	99	100	101	102	104	107	109	110	111	114
0·060	0·041	0·065	0·064	0·058	0·068	0·082	0·075	0·085	0·099	0·072	0·116	0·137	0·176	0·206
0·095	0·080	0·106	0·105	0·089	0·106	0·120	0·113	0·123	0·133	0·114	0·210	0·249	0·329	0·358
0·127		0·142	0·136	0·119	0·140	0·156	0·150	0·157	(0·167)		0·292	0·353	0·455	0·492
0·158		0·176	0·166	0·149	0·174	(0·188)	0·186	0·189			0·368	0·449	0·579	0·620
0·216		0·239	0·226	0·206	0·233		0·251	0·250			0·499	0·624	0·828	0·869
0·272		0·295	0·284	0·261	0·282		0·307	0·304			0·613	0·778	1·078	1·085
0·330		0·347	0·339	0·314	0·331		0·360	0·355			0·710	0·914	1·321	1·281
0·467		0·457	0·469	0·439	0·444		0·482	0·471			(0·925)	1·200	1·746	
0·592		0·562	0·589	0·554	0·544		0·596	0·585				1·432	2·023	
0·814		(0·749)	(0·804)				(0·802)					1·825	2·488	

In order to obtain an idea of the currents which must exist owing to the differences in density, Figs. 34 and 35 have been constructed. Fig 34 shows the topography of the surface relative to the 1000 decibar surface. Simultaneously the lines represent the lines of flow relative to the flow at a depth of nearly 1000 metres. The chart has been extended towards the west in order to include the area of the Agulhas current and the most eastern part of the Weddel Sea, from which areas similar charts have been published by Dietrich (1935) and Mosby (1934). A combination of these charts is easily undertaken. The lines of equal anomaly can be drawn across the entire Indian Antarctic Ocean from Africa to Australia, but the distances between the lines are uncertain since the stations are far apart. The picture which is presented has, therefore, a schematic character.

In the first place, it is seen that the sea surface, on the whole, slopes towards the Antarctic continent, from north to south, indicating that the surface water flows towards the east relative to the direction of flow at a depth of about 1000 metres. We find, however, some noteworthy exceptions. On the south-eastern side of South Africa we recognize the south-flowing Agulhas current, which to a great extent bends back again to the Indian Ocean. In about the same longitude, but further to the south, the east-going current is deflected towards the south. Part of it is bent around and flows westward along the Antarctic Continent, forming the southern branch of the big eddy in the Weddell Sea area, whereas another part continues towards the east along the continent. Along the very slope of the continental shelf the relative motion appears to be towards the west.

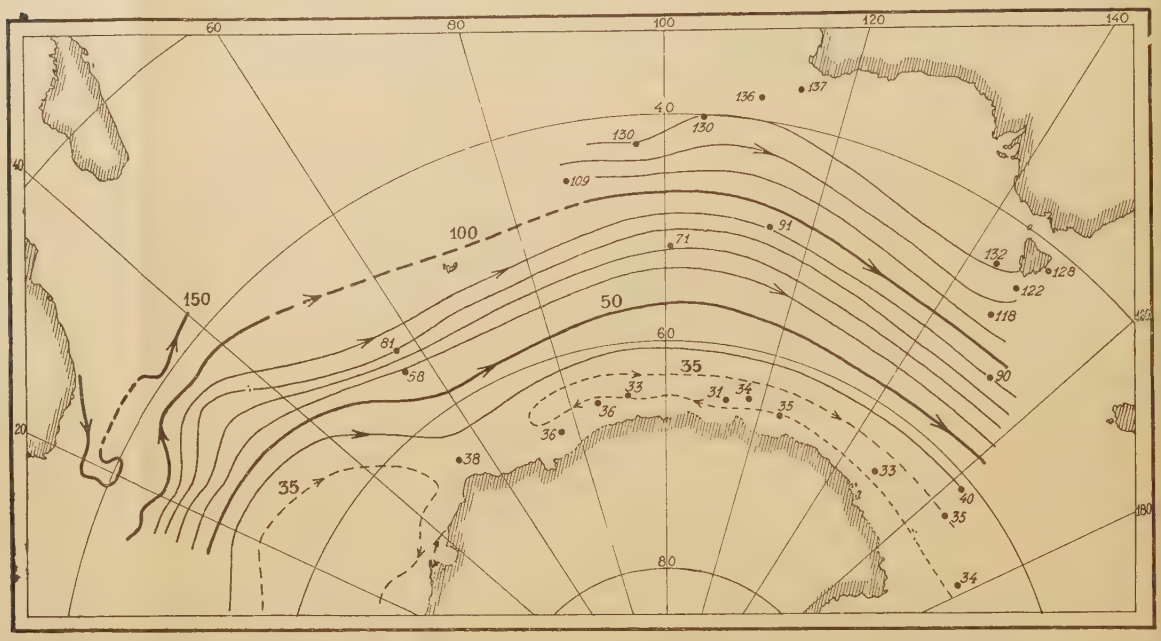


Fig. 34. The topography of the surface relative to the topography of the 1,000 decibar surface (dyn. centimetres).

The lines in Fig. 34 would represent the actual lines of flow at the surface, supposing the water at about 1000 metres to be at rest and that no wind-currents exist. None of these conditions is fulfilled. From Fig. 27, showing the distribution of the specific volume anomaly in a vertical section, it is evident that considerable differences of density exist below the 1000 metres level, the water in the northern part of the scetion being lighter than in the southern. It is, therefore, not probable that the current is zero at a depth of 1000 metres, but that it is directed towards the east at this level as well. If it were zero we would find west-going current below 1000 metres, and this is not in agreement with the character of the water.

We obtain a better representation of the actual currents which are present in the upper layer owing to the density distribution, if we consider the topography of the surface relative to the topography of the 2000 decibar surface, since the slope of the latter is, no doubt, smaller than the slope of the 1000 decibar surface. Fig. 35 shows the lines of equal anomaly 0–2000 decibar. In the figure the eastern part of the Weddell Sea area has been included (Mosby, 1934), but the Agulhas-current area has not been considered since the corresponding data from this area are lacking. It is seen that near the continent the flow relative to the flow at 2000 metres is directed towards the east from Enderby Land and eastward, but towards the west and into the Weddell

Sea on the western side of Enderby Land. Somewhere off Enderby Land the surface shows a neutral point, and to the south of this point the flow is directed away from the coast. Here ascending motion must be present, but the location of the neutral point cannot be determined exactly, and the same applies to the region of ascending motion. It seems, however, certain that somewhere along the coast ascending motion must take place.

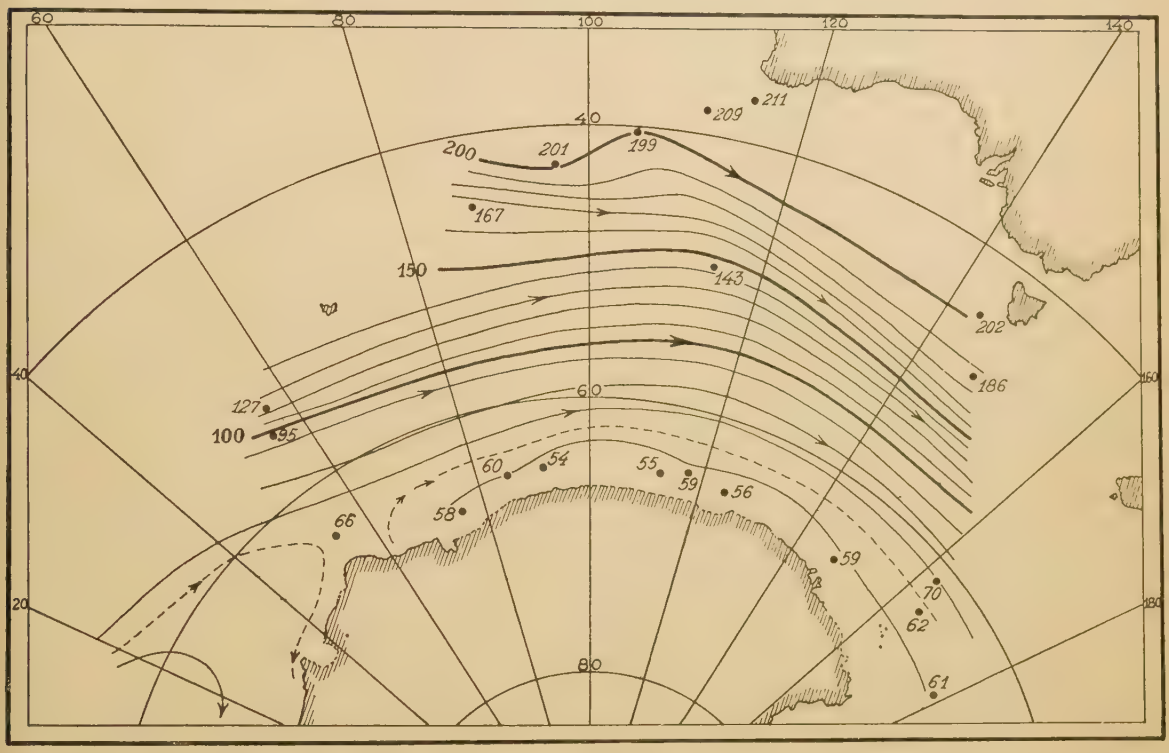


Fig. 35. The topography of the surface relative to the topography of the 2,000 decibar surface (dyn. centimetres).

We have until now disregarded the wind currents in the upper layers. Along the continent easterly winds prevail; there the wind current at the surface must therefore be directed towards the west with a component against the coast, and the total transport by the wind current must be directed towards the south. When dealing with the Antarctic upper water it was shown that the boundary between the upper water and the deep water sinks rapidly when approaching the coast (Fig. 11), from about 100 metres at a distance of less than one degree of latitude from the slope of the continental shelf to more than 600 metres very near the slope. The accumulation of Antarctic upper water on and along the shelf which this inclined position of the boundary indicates, is probably an effect of the prevailing easterly winds. The density of the upper water differs, however, so little from the density of the deep water that the effect of this displacement upon the currents which are caused by the density distribution (the convection current according to Ekman's terminology) is very small. The upper water is somewhat lighter than the deep water, and the east-going convection current is, therefore, somewhat weaker at the surface than at the upper boundary of the deep water.

At a greater distance from the coast westerly winds prevail, which near the surface produce a total water transport towards the north. Thus, off the coast we must find a region with diverging wind currents, and ascending motion must, therefore, be present somewhere below the sur-

face. Since the stability is smallest along the slope of the continental shelf it is natural to assume that this ascending motion takes place along the slope. Thus, the dynamic conditions support the conclusions which were previously drawn from the distribution of silicate and phosphate. It must, however, be underlined that conditions are not stationary. The ascending motion may

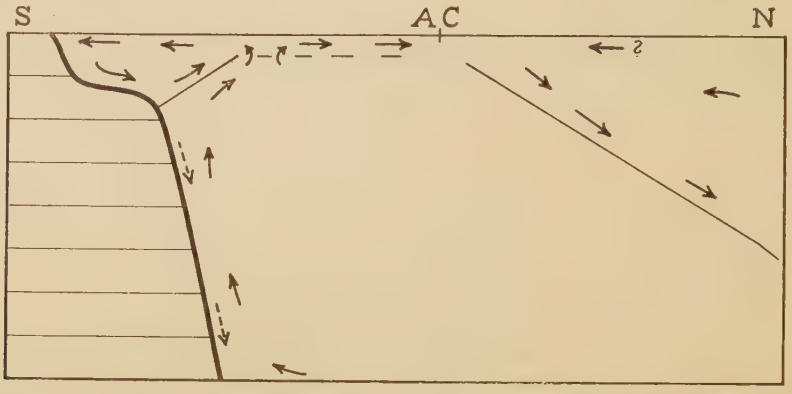


Fig. 36. Schematic representation of the north-south and vertical component of the currents off the Antarctic Continent in longitudes 60° to 150° E. The motion is directed towards the east, except perhaps within the upper layers on the continental shelf where it, owing to easterly wind, is directed to the west.

have an irregular character and occasionally sinking of exceptionally heavy upper water may take place along the slope, but the latter process is probably an intermittent one and of secondary importance. Fig. 36 has been prepared in order to give a schematic illustration of the probable vertical circulation within the region between Enderby Land in long. 50° E. and Adelie Land in 140° E.

It will not be attempted to compute the velocity of the convection current at different levels or in different regions, since the distance between the stations is so great that the computation renders only average values. It must be sufficient to mention that in general the velocity of the east-going current decreases with increasing depth, except near the continent, where it increases to a maximum near the upper boundary of the deep water. The highest surface velocities are probably found to the north of the Antarctic Convergence, where the greatest slope of the sp. volume anomaly lines occurs, and where the velocity reaches a value of at least 12 cm./sec.

An approximate value of the total transport of water between Tasmania and the Antarctic continent can be computed by means of the observations at Stations 87 and 111. The transport between two stations, A and B, reckoned from the surface to the depth is:

$$T = Lh\frac{1}{h}\int_0^h u_z dz$$

where u_z is the velocity and L the distance between the stations. From Bjerknes's theory of circulation we obtain under stationary conditions and in the absence of friction, assuming no motion at the lower isobaric surface:

$$u = \frac{(\epsilon a - \epsilon b)}{2\omega \sin\phi\, L}$$

where ϵa and ϵb represent the anomalies of the geopotential of isobaric surfaces. Thus,

$$T = \frac{1}{2\omega \sin\phi}\int_0^h (\epsilon a - \epsilon b)\, dh$$

Expressing L and h in metres and ϵ in "dynamic decimetres" we obtain the transport in cubic metres per second. When carrying out the computation we consider the anomaly difference at one given depth as equal to the anomaly difference at a pressure which, when using decibar as unit, is expressed by the same figure as the depth. If we consider the 3000 decibar surface as horizontal we obtain the following values of the eastward transport of the convection current between Tasmania and the Antarctic continent:

Layer.	Transport in m^3/sec.
0–1000 metres	98
1000–2000 „	36
2000–3000 „	10
0–3000 metres	144×10^6

Below 3000 metres the transport is, no doubt, small, and the total water mass, which to the south of Australia the convection carries towards the east is, therefore, of the order of 150 million cubic metres per second. This value compares well with the value of 110 million cubic metres per second, which Clowes (1933) has found for the eastward transport through Drake passage. The transport between Tasmania and the Antarctic continent must be expected to be greater than the transport through Drake passage, since to the south of Tasmania the current carries a considerable amount of sub-Antarctic water which branches off towards the north, mainly in the Pacific Ocean, and does not continue through Drake Passage. The value 150 million cubic metres per second can, therefore, not be essentially wrong.

11. THE DEEP WATER CIRCULATION OF THE OCEANS.

The hypothesis which the present author previously has advanced concerning the circulation around the Antarctic Continent, must, as already mentioned, be abandoned, since it was assumed that bottom water forms all along the Continent and flows towards the west, whereas the present observation shows that the bottom water is formed mainly in the Weddell Sea area from where it flows towards the east. In view of these circumstances it may be appropriate to advance another view.

From what is known now it seems that the Atlantic Ocean is the only ocean with a well developed flow of the deep water and the bottom water. Wüst (1935) has shown that within the Atlantic deep water two different types of water are met with: (1) Mediterranean water, which has a high temperature and can be traced as "upper deep water" to South Africa, and (2) North Atlantic water, which can be followed as "lower deep water" from the areas south-east of Greenland and towards the Antarctic continent. Furthermore, Wüst and Mosby (1934) have shown that the greater part of the bottom water originates in the Weddell Sea.

Thus, in the Atlantic we find three "centres of action". Firstly we have the Mediterranean area, where the salinity of the water is increased owing to evaporation. The outflowing water has, therefore, a high salinity, but it has also a high temperature, and must, therefore, spread at a moderate depth, as upper deep water. Secondly, we have the region to the south-east and east of Greenland, the Irminger Sea and neighbouring areas. Atlantic upper water, which owing to evaporation in lower latitudes has a high salinity, is carried to this region, where it is cooled off to such an extent that in some localities a water is formed which is of uniform density from the surface to the bottom. In these places the upper water may sink to great depths and renew the lower deep water. Thirdly, we have the Weddell Sea area, in which the water is cooled to freezing

point and the salinity increased by freezing of ice. In this region the heaviest water is formed, excepting the very heavy North-Atlantic bottom water, which, however, plays a small part. The Weddell Sea water contributes to the formation of the bottom water in all oceans, but is in the North Atlantic Ocean mixed with the still heavier bottom water which is formed in the northern parts of this sea, and which is related to the lower deep water of the North Atlantic.

It is interesting to note that within these three "centres of action" the increase of salinity due to evaporation or freezing is of very great importance. Evaporation and freezing are, therefore, processes which exert a dominating influence upon the deep water circulation, but evaporation becomes effective in two cases only:

(1) within a more or less closed area which communicates with the ocean through a narrow channel (The Mediterranean Sea);

(2) within an area where water which, owing to evaporation in lower latitudes, has a high salinity, is cooled in high latitudes (The Irminger Sea).

In the Indian Ocean the Red Sea is the only corresponding centre of action, but there the Red Sea water, which is found as an "upper deep water" similar to the Mediterranean water in the Atlantic, does not sink to such a great depth owing to its higher temperature, and it has not such a wide distribution, since the Red Sea is a smaller basin. In the Pacific no corresponding centres are found, and within the entire area the production of deep water and bottom water is, therefore, insignificant.

Thus, considerable quantities of deep water and bottom water are produced in the Atlantic Ocean only. In the Indian and the Pacific Oceans the deep water and the bottom water are renewed very slowly by admixture of Atlantic deep water and Antarctic bottom water. The stratospheric layers of the Indian, and especially the Pacific Oceans, are almost motionless as compared to the corresponding layers in the Atlantic Ocean.

The view which has been presented here deviates in some essential points from the previous hypothesis. According to the latter the bottom water around the Antarctic continent was supposed to flow towards the west, and the northward flow in the Atlantic was supposed to be caused by the configuration of the bottom. Now the circulation within the Atlantic Ocean is assumed to be a "free" circulation between certain "centres of action" within which deep water and bottom water are produced. Owing to this circulation, water masses of Atlantic origin are added to the Antarctic circumpolar flow, from which the deep water and bottom water in the Indian and Pacific Oceans are slowly renewed, in a manner which is still unknown.

LITERATURE.

Brennecke, W.: Die ozeanographischen Arbeiten der Deutschen Antarktischen Expedition 1911–1912 ("Deutschland"). Aus dem Archiv der Deutschen Seewarte *39* Nr. 1. Hamburg, 1921.

Clowes, A. J.: Influence of the Pacific on the Circulation in the South-West Atlantic Ocean. Nature, *131*. London, 1933.

Deacon, George E. R.: Die Nordgrenzen antarktischen und subantarktischen Wassers im Weltmeer. Ann. d. Hydr. u. mar. Met. *62* (1934). Berlin, 1934.

Dietrich, G.: Aufbau und Dynamik des südlichen Agulhasstromgebietes. Veröff. des Institutes für Meereskunde, Berlin. Neue Folge, Reihe A, Heft 27. Berlin, 1935.

Helland-Hansen, B.: Physical Oceanography and Meteorology Part I (Text). Rep. of the Sci. Results of "Michael Sars" North Atlnt. Deep-Sea Exped. 1910. Vol. I. Bergen, 1930.

Hesselberg, Th. und Sverdrup, H. U.: Die Stabilitätsverhältnisse des Seewassers bei vertikalne Verschiebungen. Bergens Museums Aarbok 1914–1915, Nr. 15. Bergen, 1915.

Mosby, Haakon: The Waters of the Atlantic Antarctic Ocean. Scient. Results of the Norw. Antarctic Expd. 1927–1928 et SQQ., instituted and financed by Consul Lars Christensen. No. 11. Det Norske Videnskaps-Akademi i Oslo. Oslo, 1934.

Möller, Lotte.: Die Zirkulation des Indischen Ozeans. Veröff. des Instituts für Meereskunde, Berlin, Neue Folge, Reihe A, Heft 21. Berlin, 1929.

Schubert, O. V.: Quantitative Untersuchungen zur Statik und Dynamik des Atlantischen Ozeans. Die Stabilitätsverhältnisse. Wiss. Erg. der Deutschen Atl. Expd. auf dem Forschungs-und Vermessungsschiff "Meteor" 1925–1927. Band VI-Zweiter Teil, 1, Lieferung. Berlin, 1935.

Sverdrup, H. U.: The Origin of the Deep-Water of the Pacific Ocean as indicated by the Work of the "Carnegie". Gerl. Beitr. z. Goph. *29*. Leipzig, 1931.

Thomsen, H.: Entstehung und Vergreitung einiger characteristicher Wassermassen in dem Indischen und südlichen Paxifischen Ozean. Ann. d. Hydr. u. mar. Met. *63* (1935). Berlin, 1935.

Wüst, Georg.: Schichtung und Zirkulation des Atlantischen Ozeans. Die Stratosphäre. Wiss. Ergebn. der Deutschen Atl. Expd. auf dem Forschungs- und Vermes-sungsschiff "Meteor" 1925–1927. Band VI, Erster Teil, Zweite Lieferung. Berlin, 1935.

LIST OF TEXT FIGURES.

Fig. 10. Characteristic T-S curves from the Indian-Australian Antarctic Ocean.

Fig. 11. Thickness in metres of the layer of Antarctic upper water near the Antarctic Continent.

Fig. 12. Temperature and salinity of the surface layer and of the sub-surface layer of maximum salinity to the north of the Antarctic Convergence, and corresponding values at the depths of 200 and 500 metres in the region of the Agulhas current.

Fig. 13. The T-S relation within the intermediate water of the Atlantic Ocean (according to Wüst) and T-S values of the Intermediate water of the Indian Ocean according to observations on B.A.N.Z.A.R.E. stations, *Discovery* stations, and *Dana* stations. T-S curves from Stations 65, 109, 110.

Fig. 14. Surface temperatures, salinities, and densities at three crossings of the Antarctic Convergence.

Fig. 15. Temperature and salinity of the deep water at 7 stations around the Antarctic Continent.

Fig. 16. Temperature and salinity at the B.A.N.Z.A.R.E. stations to the north of the Antarctic Convergence.

Fig. 17. Temperature and salinity at B.A.N.Z.A.R.E. stations near the Antarctic Continent.

Fig. 18. The T-S relation of the deep water within the Atlantic and western Indian Oceans (according to Wüst) and within the eastern Indian Ocean.

Fig. 19. Temperature and salinity of the deep water in the region of Enderby Land.

Fig. 20. T-S relation of Atlantic bottom water, according to Wüst, and temperature-salinity values of the bottom water of the Indian-Australian Antarctic Ocean.

Fig. 21. Temperature sections at right-angles to the Antarctic Continent.

Fig. 22. Temperature and oxygen values of the deep water near the Antarctic Continent according to B.A.N.Z.A.R.E. observations.

Fig. 23. Temperature and oxygen values of the deep water in the Drake passage according to *Discovery* observations.

Fig. 24. Temperature and oxygen values of the deep water near the Antarctic Continent according to *Thorshavn* observations.

Fig. 25. The salinity in a vertical section between the Antarctic Continent and Tasmania.

Fig. 26. The temperature in a vertical section between the Antarctic Continent and Tasmania.

Fig. 27. The anomaly of the specific volume ($10^5\Delta\alpha$) in a vertical section between the Antarctic Continent and Tasmania.

Fig. 28. The stability (10^8E) in a vertical section between the Antarctic Continent and Tasmania.

Fig. 29. The silicate (in mg./L) in a vertical section between the Antarctic Continent and Tasmania.

Fig. 30. The phosphate (in mg./L) in a vertical section between the Antarctic Continent and Tasmania.

Fig. 31. The silicate (in mg./L) in a vertical south-north section in long. 55° E.

Fig. 32. The phosphate (in mg./L) in a vertical, north-south section in long. 55° E.

Fig. 33. The oxygen (in ml./L) in a vertical, north-south section in long. 55° E.

Fig. 34. The topography of the surface relative to the topography of the 1,000 decibar surface (dyn. centimetres).

Fig. 35. The topography of the surface relative to the topography of the 2,000 decibar surface (dyn. centimetres).

Fig. 36. Schematic representation of the north-south and vertical component of the currents off the Antarctic Continent in longs. 60° to 150° E.

Printed at THE HASSELL PRESS, Adelaide

Contribution No. 92

Reprinted from JOURNAL OF BACTERIOLOGY
Vol. 40, No. 2, August, 1940

STUDIES ON THE THERMAL SENSITIVITY OF MARINE BACTERIA[1]

CLAUDE E. ZOBELL AND JEAN E. CONN[2]

Scripps Institution of Oceanography,[3] University of California, La Jolla, California

Received for publication January 18, 1940

There are numerous reports (Benecke, 1933, Waksman, 1934, ZoBell, 1938) on the occurrence and importance of bacteria in the sea in different parts of the world but, unfortunately, the methods of investigation used by various workers have been so widely divergent that neither the qualitative nor the quantitative results are comparable. One of the greatest variables is the temperature to which the bacteria have been subjected, although Forster (1892), Drew (1910), Berkeley (1919), and others have emphasized the extreme thermal sensitivity of marine bacteria. In fact, due to a lack of appropriate refrigeration of water baths, incubators, and other facilities while working on a boat at sea, marine bacteria have been subjected to wide ranges of temperature. This paper is concerned with the effect that this may have upon the life processes and death of the bacteria.

Only those bacteria found in the sea which will grow in nutrient sea water media but not in corresponding freshwater media, or those which have been isolated from a marine environment at places remote from possibilities of terrigenous contamination, are regarded as marine species. This distinction is made to exclude bacteria of obviously terrestrial origin with which bays, estuaries and coastal waters are contaminated. While there may be an interchange of bacteria between the land and the sea (Burke,

[1] Technical assistance in these studies was furnished by the personnel of the Works Progress Administration, Project No. 665-07-3-141.

[2] Present address, New York Agricultural Experiment Station, Geneva, N. Y.

[3] Contribution from the Scripps Institution of Oceanography, New Series No. 92.

1934) with certain bacteria common to both environments, the majority of those occurring under truly oceanic conditions are believed to be distinctive marine species (ZoBell and Feltham 1933).

EXPERIMENTAL METHODS

Samples of sea water for analysis were obtained by means of the bacteriological sampler described by ZoBell and Feltham (1934) and bottom deposits were obtained with a Trask coring tube (Hough, 1939). Radially central portions of the mud core were dissected out aseptically for bacteriological purposes. Most of the samples were analyzed shortly after collection although sometimes the urgency of other activities, rough weather or other adverse field conditions necessitated storage of the samples. Since earlier studies have revealed that the total number of bacteria in sea water (ZoBell and Anderson, 1936) as well as in mud samples (ZoBell, 1938) increases rapidly with storage, a change which is accompanied by a decrease in the number of different species discernible, the stored samples were held in the refrigerator at near 0°C. At this temperature the changes in the bacterial population are minimized, though not entirely prevented. There is no evidence that any species are killed or overgrown even after several days storage at 0°C., but many heat-sensitive species are destroyed by a few minutes exposure to temperatures exceeding 25°C. and the fastidious ones are soon crowded out when samples are stored at temperatures higher than 5°C. Prescott and Winslow (1931) have discussed the effect of storage upon water bacteria with particular reference to temperature.

Sterile sea water was used for dilution blanks. The nutrient media contained 0.2 per cent each of Bacto-peptone, proteose-peptone and beef extract and 0.002 per cent iron citrate in sea water using either 1.2 per cent agar or 10 per cent gelatin as solidifying agents. The reaction was adjusted to pH 7.6 with N/10 NaOH after autoclave sterilization. Unless otherwise stated, 10 ml. of medium was used to pour the plates and the plates were incubated for two weeks at 22°C. The colonies were counted with a Stewart colony counter using a 3.5× engraver's lens.

POURING TEMPERATURE OF THE MEDIUM

Not infrequently nutrient agar is poured into inoculated plates before it has cooled to 42°C., below which temperature it begins to congeal. (Similar concentrations of agar congeal at a somewhat higher temperature in sea water than in freshwater.) In order to ascertain to what extent the temperature of melted agar influences plate counts, samples of sea water were plated with agar at temperatures ranging from 42° to 60°C. The medium was cooled to exactly the stated temperature in a water bath and then poured into 10 cm. Pyrex Petri dishes previously inoculated with 1.0 ml. of raw sea water.

TABLE 1

Relative number of colonies developing from sea water or marine mud when plated with nutrient agar at different temperatures, the plate counts being expressed as percentages of the average plate count on media poured at 42°C.

INOCULA	NUMBER OF SAMPLES	POURING TEMPERATURE OF AGAR				
		42°C.	45°C.	50°C.	55°C.	60°C.
		per cent	*per cent*	*per cent*	*per cent*	*per cent*
Sea water	14	100	95.8	89.4	34.2	17.5
Marine mud	9	100	93.4	82.1	26.9	11.4

More bacteria developed on the medium which was poured at 42°C. than on that poured at higher temperatures. Moreover, the agreement between duplicates was better when the agar was poured at the lower temperatures. The results obtained with 14 different samples of sea water and 9 of marine bottom deposits which were plated in duplicate with nutrient agar at different temperatures are summarized in table 1. The average plate counts are expressed as ratios on a basis of the 42°C. count being 100.

The data reveal that about 95 per cent as many bacteria form colonies when the agar is plated at 45°C. as when it is plated at 42°C. and successively smaller percentages at higher temperatures. However, the experiment fails to show what percentage of the bacteria may be rendered incapable of multiplication by pouring the agar at 42°C., a temperature which is considerably

in excess of that of their environment. Since agar begins to congeal at 42°C., gelatin was used to prepare a solid medium which could be plated at lower temperatures. Gelatin is not entirely satisfactory as a solidifying agent because it is liquified by the actively proteolytic bacteria which are abundant in the sea. Therefore, gelatin plates must be counted before the slower-growing bacteria have had time to develop into macroscopically visible colonies.

The nutrient gelatin was poured at temperatures ranging from 30° to 50°C. The plates were incubated at 12°C. for a week. The relative numbers of bacteria which developed on the medium poured at each temperature are shown in table 2 which gives the

TABLE 2

Relative number of colonies developing from sea water or marine mud when plated with nutrient gelatin poured at different temperatures, the plate counts being expressed as percentages of the average plate count on media poured at 30°C.

INOCULA	NUMBER OF SAMPLES	POURING TEMPERATURE OF GELATIN				
		30°C.	35°C.	40°C.	45°C.	50°C.
		per cent	*per cent*	*per cent*	*per cent*	*per cent*
Sea water	12	100	98.6	96.5	87.5	76.2
Marine mud	16	100	97.9	91.3	83.4	67.8

average of duplicate analyses on 12 samples of sea water and 16 of marine mud.

Approximately as many bacteria developed on the gelatin medium poured at 35°C. as on that poured at 30°C. and almost as many developed on the medium poured at 40°C. However, significantly fewer bacteria developed on the medium poured at higher temperatures. It is evident from these observations that while marine bacteria are extremely sensitive to heat, they are not sufficiently so to invalidate the use of nutrient agar poured at 40° to 42°C. for estimating the abundance of bacteria in marine materials since, at their best, plate counts detect only a small percentage of the bacterial population. It is obvious, though, that the medium should be cooled at least to 42°C. before pouring to insure comparable and maximum counts because even

at this temperature certain heat-sensitive species are inactivated. If, due to the exigencies of field conditions, media are poured at temperatures exceeding 50°C., more than half of the bacteria may fail to develop. Drew (1910) reports that the bacteria from tropical waters around the Bahamas are very sensitive to temperatures as high as 40°C. and exposure at 45°C. causes the death of a large proportion of them.

In the foregoing experiments the plates themselves were at room temperature (21° to 22°C.) at the time the media were introduced. It was found that when the plates were cooled on ice prior to the introduction of the medium, plating temperatures in excess of 42°C. were less injurious. This is what might be expected because the introduced medium is cooled faster, thus subjecting the bacteria therein to the higher temperature for a shorter period of time. As revealed by the results summarized in table 3, little or no practical advantage is gained by cooling the plates on ice when the medium itself is cooled to 42°C. before pouring but the beneficial effect of the use of ice is quite pronounced when the medium is poured at higher temperatures. The use of ice to hasten the cooling of the media might save a few heat-sensitive species from destruction but for practical purposes this procedure does not increase the plate count enough to offset the disadvantages of the extra work involved and the undesirable effects of the medium congealing in the cold plate before it has been evenly distributed (Green, 1936).

Other factors which influence the effect of the pouring temperature of the medium are the type of plate, the heat-conductivity of the table upon which the plate rests and the size of the inoculum. The media are cooled faster by thick-walled Pyrex Petri dishes of high heat-holding capacity than by thin-walled ones, assuming that the dishes themselves are at a low temperature when the medium is introduced. Similarly, the media are cooled faster when the plates are resting on a foundation of concrete, metal or soapstone than on one of wood. Such factors influence the magnitude of plate counts and the agreement between duplicates.

Prescription bottles are quite widely used as a substitute for

Petri dishes for field studies. One milliliter of the appropriately diluted sample is introduced directly into 15 ml. of melted nutrient agar in the bottles cooled to 40° to 42°C. The inoculated bottles are then placed on their sides until the agar has solidified. In the initial experiments less than half as many colonies developed in prescription bottles inoculated by this procedure as when a similar medium was used in Petri dishes, probably because

TABLE 3

Relative number of colonies developing from sea water plated with nutrient agar poured at different temperatures into plates at different temperatures, the plate counts being expressed as percentages of the average plate count on media poured at 42°C. into dishes having a temperature of 21–22°C.

TEMPERATURE OF PLATE	POURING TEMPERATURE OF AGAR				
	42°C.	45°C.	50°C.	55°C.	60°C.
°C.	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*
Near 0	108	103	95	68	51
21–22	100	97	86	41	16
30	79	72	61	36	14

TABLE 4

Relative number of colonies which developed from samples of sea water or mud after being held at the stated temperature for 10 minutes, the plate counts being expressed as percentages of the plate count of material held for ten minutes at 20°C.

INOCULA	NUMBER OF SAMPLES	EXPOSURE TEMPERATURE						
		20°C.	30°C.	40°C.	50°C.	60°C.	80°C.	100°C.
		per cent	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*
Sea water	10	100	81.3	21.9	6.8	3.0	0.2	+
Marine mud	10	100	68.5	18.3	10.3	5.2	0.7	+

the prescription bottles cool so slowly. By immersing them to the neck for thirty seconds in ice water immediately after inoculating, almost as many colonies developed in prescription bottles as in Petri dishes.

Marine bacteria are not unique in their susceptibility to the pouring temperature of nutrient agar because the senior author found that the bacteria indigenous to Lake Mendota (a freshwater lake in Wisconsin) are similarly heat-sensitive. Using the pre-

scription bottle technique, two to five times as many bacteria developed when the bottles were quickly cooled after inoculation by immersion in cold water as when they were merely permitted to cool on the table top, although in both cases the medium was cooled to 40° to 42°C. before inoculation.

The use of pre-solidified agar as advocated by Anderson and Stuart (1935) obviates the necessity of exposing the bacteria to the temperature of melted agar. While, statistically, the counts obtained by this procedure compare favorably with plate counts obtained by the conventional technique, there is a greater divergence of duplicates and many time-consuming precautions must be exercised to prepare satisfactory plates.

THERMAL DEATH POINT

The temperature tolerance of marine bacteria was determined using thermal death point technique. For this purpose 2.0 ml. portions of recently collected sea water or appropriately diluted mud samples were placed in 6 ml. serological tubes. The use of the small thin-walled tubes reduced to a minimum the time required to change the temperature of the contents. Pairs were immersed in water baths ranging in temperature from 20° to 100°C. After exactly ten minutes the tubes were transferred to ice water and 1.0 ml. of the heated suspension was spread uniformly over the surface of pre-solidified nutrient agar in Petri dishes. The plates were incubated at 12°C. for two weeks. Table 4 shows the average number of colonies which developed from samples of sea water and marine mud treated in this manner.

There is no evidence to suggest that any of the bacteria are injured by ten minutes exposure to a temperature of 20°C. regardless of the temperature of the environment from which they were obtained. However, about one-fourth of the bacteria were rendered incapable of multiplication in ten minutes at 30°C. and only one-fifth of them survived after being held for this period of time at 40°C. Direct microscopic observations of the material showed that the heat treatment had not merely caused the bacteria to clump together or to adhere to the walls of the sero-

logical tubes which would have reduced the plate counts. Moreover, as will be discussed below, the respiration of the bacteria was impaired by the heat treatment.

In general, the bacteria from bottom deposits were found to be somewhat more heat-sensitive than those occurring in sea water. A few heat-tolerant spore-forming bacteria were found in nearly all of the samples, there being more of these in mud than in water. Most of the bacteria which survived temperatures higher than 40°C. proved to be spore formers. Not many of the spore formers survived at 80°C. and too few survived boiling for ten minutes to warrant the numerical expression of an average from the available data.

TABLE 5

Number of pure cultures which multiplied after being held at the stated temperature for 10 minutes

DESCRIPTION OF CULTURES	EXPOSURE TEMPERATURE						
	20°C.	30°C.	40°C.	50°C.	60°C.	80°C.	100°C.
"C_1" from water	25	24	9	3	0	0	0
"C_1" from mud	25	21	11	5	1	1	0
Stock cultures	78	78	36	14	8	6	2

The temperature tolerance of several pure cultures of marine bacteria was tested by noting their ability to reproduce after being heated. Nutrient sea-water broth was inoculated and distributed in serological tubes. Pairs of these were held in water baths at different temperatures for ten minutes and then cooled immediately in ice water, after which the bacteria were tested for viability. Table 5 shows the number of cultures which multiplied following this treatment.

The cultures designated "C_1", are colonies differing superficially from each other, fished directly from pre-solidified nutrient agar which had been inoculated with freshly collected samples of sea water or marine mud and incubated at 12°C. At no time were these organisms subjected to temperatures higher than 12°C. until they were tested for their temperature tolerance. The "stock" cultures, all differing either morphologically, culturally

or physiologically from each other, have been isolated over a period of years from sea water or other marine materials. They have been sub-cultured many times and maintained on sea-water agar slants in the refrigerator at 0° to 4°C.

Only five cultures out of the 128 tested failed to grow after being held at 30°C. for ten minutes but many of them multiplied less rapidly, indicating that while all of the individuals comprising any one culture had not been killed, many of the individuals were injured. This was confirmed later by plate counts on the cultures and observations on the respiration of heat-treated cultures. It is noteworthy that over half of the pure cultures were killed in 10 minutes at 40°C. Similarly Bedford

TABLE 6

Oxygen consumed by suspensions of marine bacteria in two hours at 20°C. after being heated to the stated temperature for ten minutes and the number of viable bacteria in the heated suspensions

	EXPOSURE TEMPERATURE			
	20°C.	30°C.	40°C.	50°C.
Oxygen uptake ($mm.^3$)	0.92	0.54	0.19	0.04
Bacteria per ml. × 100,000	267	184	51	9

(1933) found that 37°C. was lethal for 40 of the 71 cultures of marine bacteria with which he was working.

According to Bronfenbrenner *et al.* (1939) the respiration of bacteria is a better criterion of their viability than their ability to reproduce in a given medium. Studies on the oxygen uptake of suspensions of marine bacteria demonstrated that many were rendered incapable of respiration by 10 minutes exposure at 30°C. The tests were made by pipetting 2.0 ml. of a heavy suspension of a 24-hour old enrichment culture of mixed marine microflora into Barcroft respirometer flasks. Duplicates of each were held in water baths at 20°, 30°, 40° and 50°C. for ten minutes, after which they were cooled immediately to 20°C. After placing 0.2 ml. of 10 per cent KOH solution in the inset the respirometer flasks were fitted to the manometers and the oxygen uptake of each suspension was noted after two hours at 20°C.

Appropriate dilutions of each suspension were plated on nutrient agar to determine the number of viable cells. The results are summarized in table 6.

It will be observed that the decrease in the number of viable bacteria as indicated by plate counts is proportional to the decrease in the oxygen uptake of the heat-treated bacteria. Similar observations were made on four different heat-sensitive pure cultures which failed to multiply after being held at 40°C. for ten minutes. The loss of the ability of heated cultures to consume oxygen indicates that the respiratory enzymes of the bacteria have been inactivated. According to Edwards and Rettger (1937) the maximum temperature tolerance of bacteria is related to the minimum temperature at which their respiratory enzymes are destroyed.

OPTIMUM TEMPERATURE OF INCUBATION

In spite of the fact that Standard Methods of Water Analysis (1933) is concerned primarily with the bacteria which are of sanitary significance and which may differ markedly from the autochthonous microflora of natural waters, many bacteriologists have taken literally the instructions to count agar plates at either 20° or 37°C. when analyzing ocean, lake or river water. Most frequently the plates have been incubated at some intermediate temperature, namely, 25° or 30°C. We have studied the effect of the temperature of incubation upon plate counts by inoculating Petri dishes in groups of 14 each with 1.0 ml. of sea water or marine mud. Duplicate plates from each sample were incubated at 4°, 12°, 18°, 22°, 25°, 30° and 37°C. After different periods of incubation the colonies were counted. Table 7 shows the average results obtained with ten samples of sea water and four of marine mud. The colony counts were calculated as percentages of the maximum colony count, assuming the latter to be the colony count on plates incubated at 18°C. for 18 days. As a matter of fact the maximum number of colonies appeared on only half of the plates incubated at 18°C. for 18 days. The maximum counts of four samples occurred on plates incubated at 12°C. and the maximum counts of the other three samples were on plates

incubated at 22°C. Results with water and mud samples were almost the same.

For the first few days of incubation the most colonies were found on plates incubated at 25° or 30°C., but after seven to ten days the most colonies were found on plates incubated at 12° to 22°C. The bacteria which multiply at the higher temperatures do so more rapidly and hence appear earlier as colonies than those incubated at lower temperatures. As a rule the colonies found on the plates incubated at the higher temperatures are larger than those growing at lower temperatures and give the former

TABLE 7

Relative number of colonies appearing on nutrient agar incubated for different periods of time at different temperatures, the plate counts being expressed as percentages of the average plate count after 18 days at 18°C.

INCUBATION TIME	INCUBATION TEMPERATURE						
	4°C.	12°C.	18°C.	22°C.	25°C.	30°C.	37°C.
days	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*
2	0	18	30	36	41	44	8
4	0	28	41	60	65	61	12
7	4	46	67	82	78	69	12
10	9	67	91	96	84	71	13
14	17	90	98	97	85	70	
18	26	97	100	95	82	63	
21	33	98	96	87	74	53	

plates the superficial appearance of having more colonies. The decrease in the counts after two weeks on plates incubated at 25°C. or higher is due to the merging of colonies and the liquefaction of the agar by certain bacteria, thereby obliterating the surrounding colonies. Very few colonies developed on the plates incubated at 37°C.

The results confirm previous experiments on the thermal sensitivity of marine bacteria and show that, in general, media inoculated with sea water or marine sediments should not be incubated at temperatures exceeding 22°C. The greatest number of different species can be detected on plates incubated at 12°C. or lower, presumably because fewer heat-sensitive species are

inactivated and apparently all of them can grow, though slowly, at 4° to 12°C. Moreover, the lower temperatures seem to favor pigment production (Hess, 1933a) and as pointed out by ZoBell and Feltham (1934) most marine bacteria are chromogenic under favorable conditions. However, due to the slowness with which colonies form at relatively low temperatures, the maximum number of visible colonies will be found on plates incubated at 18° to 22°C. for a week or two. Except for special purposes it is not feasible to incubate plates for several weeks before counting.

DISCUSSION

Since the temperature of the ocean is monotonously constant with over 80 per cent of the water and bottom perpetually colder than 5°C., it is not surprising to find that marine bacteria are extremely thermo-sensitive. It so happens that the critical point for the majority of them is near the temperature at which nutrient agar begins to congeal. While too few bacteria are killed when the medium is properly cooled to invalidate the use of plating procedures for estimating bacterial populations, it should be emphasized that prolonged exposure at 40° to 42°C., or instantaneous exposure at temperatures a few degrees higher, is lethal for a large percentage of the bacteria from the sea and perhaps from lakes also.

Anomalously the optimum temperature for the multiplication of marine bacteria in the laboratory is several degrees higher than the environment inhabited by them. Though coming from an environment which is for the most part considerably colder than 12°C., the optimum temperature for maximum plate counts of bacteria from the sea is between 12° and 22°C. The pure cultures which have been studied have temperature optima ranging from 18° to 37°C., the range for the majority being 18° to 25°C. This has been found to be true of cultures which were isolated from plates incubated at 12°C. and which had not been subjected to higher temperatures until the tests were made. Working with 71 species of bacteria from the northern Pacific Ocean, most of which were concerned with the spoilage of fish at refrigeration temperatures, Bedford (1933) found that none of them had

optima lower than 20°C. Too many intrinsic as well as extrinsic factors are involved which influence the temperature tolerance of bacteria to speculate at this time why certain bacteria have temperature optima which are several degrees higher than the environment inhabited by them.

Bacteria which are transferred directly from their native habitat to artificial media are subjected to many abrupt environmental changes besides temperature but the inimical effect of the adverse condition will probably be proportional to the temperature in accordance with the R.G.T. or van't Hoff rule. However, if the bacteria survive the shock of transplantation and start to multiply, the resulting cultures are more tolerant of laboratory conditions in general, including temperature extremes which may be because, as expounded by Sherman and Cameron (1934), physiologically old cells withstand adverse conditions better than young ones. Consequently the temperature tolerance seems to increase and the most tolerant individuals will soon predominate in the culture as the less tolerant ones fail to multiply or perish, or as stated by Reimann (1937), "an environment unfavorable to one of two mutants will cause the elimination of one and permit the growth of the other." It may be for this reason that Kluyver and Baars (1932) maintain that the longer a culture has been in the laboratory the less adaptive ability it possesses. Incidentally, like the experience of Casman and Rettger (1933) with members of the "*subtilis* group," our attempts to acclimate marine bacteria to temperatures higher than the maximum of 3- or 4-week old sub-cultures have been unsuccessful.

There is no evidence to indicate that temperatures as low as 0° to −5°C. injure marine bacteria although according to Hess (1933b), they slowly die at −16°C. Most of them multiply and are otherwise physiologically active until the water essential to chemical reactions is removed by solidification due to freezing. ZoBell (1934) reports that 76 out of 88 different species of marine bacteria multiplied slowly at 0° to −4°C. Bedford (1933) found that all of his 71 species except three grew at 0°C. and 23 of them grew at −5°C. Neither Bedford nor the senior author have

found true psychrophiles, or cultures which grow best at relatively low temperatures, but Hess (1933b) gives 5°C., as the optimum temperature for the multiplication of the marine bacteria which he has studied. Berry and Magoon (1934) who have been working with microorganisms which grow at sub-zero temperatures question the existence of a true cold-loving or psychrophilic flora.

SUMMARY

Many of the bacteria occurring in sea water and marine sediments are sensitive to the plating temperature of nutrient agar, there being significantly fewer which formed colonies on agar plated at 45°C. or above than on that plated at 42°C. There were only 81 to 83 per cent as many colonies which developed on nutrient gelatin plated at 45°C. as on that plated at 30°C.

Heating samples of sea water and mud to 30°C. for ten minutes killed around 25 per cent of the bacteria, and only 20 per cent of the bacteria survived 40°C. for ten minutes.

A diminution of the oxygen uptake of suspensions of heat-treated bacteria indicated that the respiratory enzymes of some forms are inactivated by temperatures as low as 30°C.

Nutrient agar inoculated with sea water or marine sediments yields maximum colony counts when incubated at 18° to 22°C. for a week or two. Very few colonies develop on plates incubated at 30° to 37°C.

Most of the bacteria isolated from the sea grow best at temperatures which are considerably higher than the marine environment inhabited by them. Although nearly all marine bacteria multiply slowly at near zero temperatures, true psychrophiles have not been found.

The authors are indebted to Sydney C. Rittenberg for many timely suggestions and to Catharine B. Feltham, Frances E. Sparks, and Charles C. Teter for technical assistance.

REFERENCES

Anderson, E. H., and Stuart, C. A. 1935 A quantitative differential method for counting mixed cultures of bacteria. J. Bact., **30**, 207–209.

BENECKE, W. 1933 Bakteriologie des Meeres. Abderhalden's Handb. biol. Arbeitsmethoden, **404**, 717–872.

BEDFORD, R. H. 1933 Marine bacteria of the northern Pacific Ocean. The temperature range of growth. Contrib. Can. Biol. Fisheries N. S. **7**, 431–438.

BERKELEY, C. 1919 Study of marine bacteria. Strait of Georgia, B. C. Trans. Roy. Soc. Can., **13**, 15–43.

BERRY, J. A., AND MAGOON, C. A. 1934 Growth of microorganisms at and below 0°C. Phytopathology, **24**, 789–796.

BRONFENBRENNER, J., HERSHEY, A. D., AND DOUBLY, J. 1939 Evaluation of germicides by a manometric method. J. Bact., **37**, 583–597.

BURKE, V. 1934 The interchange of bacteria between fresh water and the sea. J. Bact., **27**, 201–205.

CASMAN, E. P., AND RETTGER, L. F. 1933 Limitation of bacterial growth at higher temperatures. J. Bact., **26**, 77–123.

DREW, G. H. 1910 On the precipitation of calcium carbonate in the sea by marine bacteria, and on the action of denitrifying bacteria in tropical and temperate seas. J. Marine Biol. Assoc. United Kingdom, **9**, 479–524.

EDWARDS, O. F., AND RETTGER, L. F. 1937 The relation of certain respiratory enzymes to the maximum growth temperatures of bacteria. J. Bact., 34, 489–515.

FORSTER, J. 1892 Ueber die Entwickelung von Bakterien bei niederen Temperaturen. Zentr. Bakt. Parasitenk., **12**, 431–436.

GREEN, G. 1936 Experiments to devise a better procedure for making bacterial counts than outlined in Standard Methods. Ohio Conf. Water Purification, **18**, 77–87.

HESS, E. 1933a Cultural characteristics of marine bacteria in relation to low temperatures and freezing. Contrib. Can. Biol. Fisheries, N. S. **8**, 459–474.

HESS, E. 1933b Effects of low temperatures on the growth of marine bacteria. Contrib. Can. Biol. Fisheries, N. S. **8**, 489–505.

HOUGH, J. L. 1939 Bottom-sampling apparatus. Recent Marine Sediments. Bull. Am. Assoc. Petroleum Geol., Tulsa, Okla., 629–664.

KLUYVER, A. J., AND BAARS, J. K. 1932 On some physiological artefacts. Proc. Acad. Sci. Amsterdam, **35**, 1–11.

PRESCOTT, S. C., AND WINSLOW, C.-E. A. 1931 Elements of Water Bacteriology. John Wiley and Sons, New York, pp. 6–37.

REIMANN, H. A. 1937 The significance of bacterial variation. J. Bact., **33**, 513–523.

SHERMAN, J. M., AND CAMERON, G. M. 1934 Lethal environmental factors within the natural range of growth. J. Bact., **27**, 341–348.

Standard Methods of Water Analysis. 1933 Standard Methods for the Examination of Water and Sewage. Am. Pub. Health Assoc., New York, 180 pp.

WAKSMAN, S. A. 1934 The distribution and conditions of existence of bacteria in the sea. Ecol. Monographs, **4**, 523–529.

ZOBELL, C. E. 1938 Studies on the bacterial flora of marine bottom sediments. J. Sedimentary Petrology, **8**, 10–18.

ZoBell, C. E. 1934 Microbiological activities at low temperatures with particular reference to marine bacteria. Quart. Rev. Biol., **9**, 460–466.

ZoBell, C. E., and Feltham, C. B. 1933 Are there specific marine bacteria? Proc. Pacific Sci. Congr. 5th Congr., Can., **3**, 2097–2100.

ZoBell, C. E., and Feltham, C. B. 1934 Preliminary studies on the distribution and characteristics of marine bacteria. Bull. Scripps Inst. Oceanog., Univ. Calif., Tech. Ser., **3**, 279–296.

ZoBell, C. E., and Anderson, D. Q. 1936 Observations on the multiplication of bacteria in different volumes of stored sea water and the influence of oxygen tension and solid surface. Biol. Bull., **71**, 324–342.

Contribution No. 93

COMPOSITION OF SEA WATER*

By

JOHN LYMAN AND RICHARD H. FLEMING

Scripps Institution of Oceanography
La Jolla, California

The principle of constant ratios between the salts in ocean water unaffected by land drainage was laid down by Forchhammer in 1864, and firmly established by Dittmar (1884). Dittmar's examination of 77 samples, collected from all the oceans of the world by H.M.S. *Challenger* in 1873–76, was so comprehensive, and his results so consistent, that some of his values are used to this day. Most estimates of the composition of sea water are based fundamentally on Dittmar's work, since subsequent individual investigations have usually been restricted to the determination of one or a few of the major constituents and the establishment of the ratios of these constituents to the chlorinity. In view of the number of such values now available it was considered of interest to prepare a revised table for the composition of ocean water. Also the more accurate methods of analysis now in use make it possible to consider the composition with greater detail. As Dittmar's values have formed the basis of such estimates, it is necessary to consider the effect on his original results of the use of more nearly exact values for atomic weights.

In order to recalculate Dittmar's values with the present accepted atomic weights, the methods by which the various constituents were determined must be taken into account. It is of course implied that the analytical methods were in themselves accurate. Table I compares the atomic weights used by Dittmar with the 1939 International values (Baxter *et al.*, 1939). In the case of potassium, Dittmar used two different values, 39 when computing the results of potassium determinations, and 39.13 when weighing KCl as a standard for chloride titrations. Table II gives the percentage composition of the salts in sea water as reported by Dittmar (1884, p. 203), the factors by which they were calculated from his weighings, and the result of recalculating these percentages with 1939 atomic weights. Dittmar's

* Contribution of the Scripps Institution of Oceanography, new series, no. 93. Paper presented at the Sixth Pacific Science Congress, San Francisco, 1939.

Reprint from SEARS FOUND. JOURN. MAR. RES.

values for calcium oxide and bromine were obtained, not from the entire 77 samples, but from three composite *Challenger* samples and a fourth sample collected near Arran, Scotland. Furthermore, it should be pointed out that sodium was not determined directly, but was estimated by summing the equivalents and calculating the sodium from the deficiency of basic constituents below acidic constituents. Hence any change in the other constituents automatically changes the amount of sodium. Dittmar does not state how he standardized the HCl used in his carbonic acid determinations, but the amount is

TABLE I

Comparison of Atomic Weights

	Dittmar, 1884	*International, 1939*
Ag	107.93	107.880
Ba	137	137.36
Br	79.95	79.916
C	12	12.010
Ca	40	40.08
Cl	35.46	35.457
K	39	39.096
and	39.13	
Mg	24	24.32
Na	23	22.997
O	16	16.0000
P	31	30.98
Pt	198	195.23
S	32	32.06

so small that revised atomic weights would introduce a negligible correction.

A complete analysis of water, for those constituents which bear a virtually constant ratio to the total salt, can be obtained from determination of a single one of these components. It is convenient to refer to these as the *major constituents* of sea water. The major constituent most easy to determine accurately is the silver-precipitating halides, and for this reason the other elements are expressed as a function of chlorinity. Chlorinity, as defined by Knudsen (1902), was the weight in grams (*in vacuo*) of the chlorides contained in one kilogram of sea water (likewise measured *in vacuo*) when all the bromides and iodides have been replaced by chlorides; in other words, the result given directly by the silver nitrate titration. To this definition must be added that the titration results be calculated with the Hydrographical Tables of Knudsen (1901, pp. 23–34) using Copen-

hagen Normal Water as the standard. *It is desirable to maintain an unvarying international standard for chlorinity, independent of atomic weights, in order that the apparent chlorinity of the oceans shall not change as revisions in atomic weights change gravimetric factors.* The Normal Water prepared by the Hydrographic Laboratories of Copenhagen has fulfilled this function. As pointed out by Matthews (Deacon, 1933), all batches of Normal Water have been referred to an original KCl primary standard calculated with 1902 atomic weights; that is, chlorinity as originally defined was identical with the volumetric chlorine-equivalent as calculated with 1902 atomic weights.

TABLE II

PERCENTAGE COMPOSITION OF SEA WATER SALTS AS REPORTED BY DITTMAR, AND AS CALCULATED FROM HIS RESULTS USING 1939 ATOMIC WEIGHTS

	Dittmar, 1884	*Factor used in calculation*	*Dittmar, 1939 atomic weights*
Cl	55.292	Cl/KCl	55.262
Br	0.1884	Br/(Br − Cl)	0.1882
SO_3	6.410	$SO_3/BaSO_4$	6.397
CO_2	0.152	$CO_2/HCl \cdot HCl/x$	0.152
CaO	1.676	weighed directly	1.674
MgO	6.209	$MgO/Mg_2P_2O_7$	6.237
K_2O	1.332	K_2O/Pt	1.353
Na_2O	41.234	by difference	41.224
	112.4934	Sum	112.4872
	12.4934	oxygen-equivalent of halide	12.4872

Jacobsen and Knudsen (1940) have established a permanent standard for chlorinity identical with the previous one but independent of the store of Normal Water at Copenhagen. The mass of silver required to precipitate completely the halogen in one kilogram of Normal Water of 19.381 ± 0.001‰ chlorinity was found to be 58.9943 ± 0.0008 grams. The new definition of chlorinity is expressed by Cl ‰ = 19.381/58.9943 = 0.3285234 Ag ‰. The 1939 atomic weight ratio Cl/Ag is 35.457/107.880 or 0.328671. Thus the chlorine-equivalent, based on 1939 atomic weights, is 1.00045 Cl ‰. For Copenhagen Normal Water labelled 19.384 ‰ the chlorine equivalent would be 19.393 grams per kilogram. Deacon (1933), as calculated by Matthews, actually found 19.394 as the chlorine-equivalent of such a water, using NaCl as a primary standard, while Thompson and Wirth (1931) found in the same way 19.378 for a water labelled 19.368 ‰ chlorinity.

Table III compares the ratios to chlorinity of the other constituents in sea water of 19.000 ‰ chlorinity as calculated from Dittmar's results in the manner previously explained, with the best values of more recent investigations. The chlorinity in each case has been adjusted to that of Copenhagen Normal Water.

TABLE III

COMPARISON OF DITTMAR'S RATIOS WITH PRESENT BEST VALUES, AND COMPOSITION OF SEA WATER HAVING CHLORINITY 19.000°/₀₀

Ion	*Ratio to chlorinity (Dittmar)*	*Ratio to chlorinity (best value)*	*Authority*	*Equivalents per kilogram*	*Weights per kilogram*
Cl	0.99894	0.99894	Dittmar (1884) and Jacobsen and Knudsen (1940)	0.53529	18.9799
Br	.00340	.00340	Dittmar (1884)	.00081	.0646
SO_4	.1388	.1394	Thompson, Johnston and Wirth (1931)	.05514	2.6486
HCO_3	.00760	.00735	Revelle (1936)	.00229	.1397
F	—	7×10^{-5}	Thompson and Taylor (1933)	.00007	.0013
				0.59360	
Ca	.02163[1]	.02106	Kirk and Moberg (1933) and Thompson and Wright (1930)	.01996	.4001
Mg	.06801	.06695	Thompson and Wright (1930)	.10460	1.2720
K	.02029	.02000	Thompson and Robinson (1932)	.00972	.3800
Sr	—	.000702	Webb (1938)	.00030	.0133
				0.13458	
Na	.5530	.5556	By difference	.45902	10.5561
				0.59360	
H_3BO_3	—	.00137	Harding and Moberg (1933) and Igelsrud, Thompson and Zwicker (1938)		.0260
					34.4816

[1] This ratio of Dittmar's is for calcium plus strontium, determined gravimetrically as oxide. The calcium and strontium best values would be 0.02165 if calculated on this basis.

The ratios for chlorine to chlorinity and bromine to chlorinity have been calculated from Dittmar's bromine : chlorinity ratio, and from the factor 1.00045 just derived. At 19.000 ‰ chlorinity, we obtain 18.9799 grams of chlorine and 0.0646 grams of bromine per kilogram. This bromine is equivalent to $0.0646 \times 35.457/79.916 = 0.0287$ grams

of chlorine, so the total chlorine-equivalent is 19.0086 and the ratio to chlorinity 19.0086/19.0000 = 1.00045.

In order to make it possible to consider the sum of all the constituents of sea water, some of the ratios of other constituents to chlorinity have been carried to a number of figures probably not justified by the accuracy of the procedures by which they were determined. In the following discussion, unless otherwise stated, the units used are grams per kilogram of sea water.

The sulfate : chlorinity ratio for a series of samples from various oceans was found by Thompson, Johnston and Wirth (1931) to be 0.1395; corrected for buoyancy in weighing, this is 0.1394. Revelle (1936) found as the base ratio for surface sea water of the northeast Pacific 0.1235 m.eq./liter per Cl ‰. Using a mean density of 1.025 and *assuming all the base to be in the form of bicarbonate,* we obtain a weight ratio $HCO_3/Cl = 0.0735$. Fluorine in sea water was determined by Thompson and Taylor (1933), who found fluorine : chlorinity $= 7 \times 10^{-5}$.

Thompson and Wright (1930) found 0.02150 gravimetrically for the calcium : chlorinity ratio for water of the northeast Pacific. Corrections for the buoyancy in weighings, a slight revision in the atomic weight of calcium, and the fact that NaCl was used as a primary Cl standard, cancel almost exactly. Kirk and Moberg (1933) found 0.02154 volumetrically for water of the same region, and here again, changes in atomic weights of carbon and calcium cancel. Webb (1938), however, has pointed out that strontium in sea water is chemically indistinguishable from calcium, and leads to a high value for the apparent calcium. With a calcium : strontium ratio of 30 : 1 (Desgrez and Meunier, 1926; Thomas and Thompson, 1932), these calcium : chlorinity ratios become respectively 0.02090 and .02122, their mean 0.02106, and the mean strontium : chlorinity ratio, 0.000702.

A magnesium : chlorinity ratio of 0.06694 is reported by Thompson and Wright (1930). This is subject to the same buoyancy and chlorinity corrections as their calcium ratio and furthermore to a change in the gravimetric factor resulting from a revision in the atomic weight of phosphorus, becoming finally 0.06695. Potassium is extremely difficult to determine in sea water. Potassium : chlorinity = 0.02000 was obtained by Thompson and Robinson (1932, p. 68) as an average of the values in the literature up to their time, and the recent result of Webb (1939) of 0.02009 ± 0.00020 is in good agreement with this. For sodium we prefer to follow Dittmar and calculate sodium as the deficiency of the other positive ions below the negative ions. The result yielded by this method, sodium : chlorinity = 0.5558, compares

well with the recent value of Webb (1939) from direct analysis, 0.5549 $\pm$ 0.0010, and is somewhat higher than the average given by Thompson and Robinson (1932, p. 174) of 0.5509.

Boric acid, which we assume not to be ionized in sea water to any appreciable extent, has been determined by Harding and Moberg (1933) and Igelsrud, Thompson and Zwicker (1938). The former found boron : chlorinity = 0.000239 by weight; the latter 0.0223 mg.at./unit Cl ‰, which is 0.000241 by weight; the mean, 0.000240 is equivalent to a boric acid : chlorinity ratio of 0.00137.

Several analyses of north Pacific sea water have recently appeared (Wentworth, 1939; Miyake, 1939). Lack of sufficient information as to the methods of analysis makes it difficult to evaluate the accuracy of these determinations, and we accordingly have not included them in preparing Table III.

The sum of all the major constituents in sea water of 19.000‰ chlorinity will now be considered. Knudsen (1902) defined salinity as the weight in grams (*in vacuo*) of the solids that can be obtained from one kilogram of sea water (likewise measured *in vacuo*), when all the bromides and iodides are converted to chlorides, the carbonates to oxides, and the remainder dried at 480° to constant weight. If we take the values given in Table III and convert the bromide to chloride and the bicarbonate to oxide (Table IV), we arrive at a value of 34.3243 for salinity, as compared with 34.325 derived from Knudsen's equation given below.

TABLE IV

Calculation of Salinity

0.1397	HCO_3 =	0.0183	O	Total salt	34.4816
.0646	Br =	.0287	Cl		.1573
0.2043		0.0470		Salinity	34.3243
.0470				Salinity from Knudsen's Tables	34.325
0.1573					

It should be emphasized that the ratios just presented hold good only at chlorinities near 19.00 ‰. Knudsen (1901) in fitting a straight line to his nine direct salinity : chlorinity determinations, obtained the expression S ‰ = 0.030 + 1.8050 Cl ‰, which implies that water having a negligible chlorinity still contains carbonates (expressed as oxides) and sulfates to the extent of 0.030 ‰. Hence the ratios of the major constituents to chlorinity depend on chlorinity. An explanation for this is easily found in the well-known observation

that river water contains more carbonate than sulfate and more sulfate than chloride. Since river water likewise contains more calcium than magnesium, and more magnesium than sodium or potassium, it would be expected that the ratios of carbonate, sulfate, calcium and magnesium to chlorinity all increase with decreasing chlorinity.

This has been shown to be true in the case of carbonate by Mitchell and Solinger (1934), but their ratios at low chlorinities are extremely variable. For the sulfate data from the Baltic, corrected for buoyancy, of Thompson, Johnston and Wirth (1931), the method of least squares yields a straight line, $SO_4 = 0.0061 + 0.1391$ Cl ‰. There are no data for magnesium which can be used in this way. For calcium, Gripenberg (1937) has some very interesting results from the Baltic. She shows that four separate water masses can be distinguished in this area on the basis of their calcium : chlorinity relationships. These yield four straight lines for calcium as a function of chlorinity, the constant term ranging from 0.0019 to 0.0226 and the slope from 0.0258 to 0.0204. The two Baltic stations used by Knudsen to determine the chlorinity : salinity relationship are located near some of

TABLE V

Calculation of the Composition of the Average Baltic Water with Which the Sea Water of Knudsen's Tables is Diluted

$S = 0.030 + 1.8050$ Cl (Knudsen, 1901)

$SO_4 = 0.0061 + 0.1391$ Cl (after Thompson, Johnston and Wirth, 1931)
$Ca = 0.0154 + 0.02025$ Cl (after Gripenberg, 1937)

$Mg/24.32 + .0154/40.08 = O/16 + .0061/96.06$ ..... (1)
$Mg + 0.0154 + O + .0061 = 0.0300$ ..... (2)

Mg	0.0020	Mg	0.0020	Mg	0.0020	$CaCO_3$	0.0385
Ca	0.0154	Ca	.0154	Ca	.0154	$MgCO_3$	.0017
SO_4	.0061	SO_4	.0061	SO_4	.0061	$MgSO_4$	.0076
O	.0065	CO_3	.0243	HCO_3	.0493		
	0.0300		0.0478		0.0728		0.0478

$Mg = 0.0020 + 0.06684$ Cl ‰ ..... (3)
$HCO_3 = 0.0493 + 0.004755$ Cl ‰ ..... (4)
$\Sigma = 0.073 + 1.8110$ Cl ‰ ..... (5)

Knudsen's equation gives the limiting concentration of salts other than chlorides as 0.030 ‰, the carbonate being weighed as oxide. Limiting values for SO_4 and Ca were found as described in the text. Two simultaneous equations (1) and (2) are now written, the first ionic, the second stoichiometric. Solution of these gives the limiting values for Mg and HCO_3, from which in turn are found (3), (4) and (5).

Gripenberg's stations, and by using her calcium values for these and the ratio already given for 19.000 ‰ chlorinity, the equation $Ca = 0.0154 + 0.02025\ Cl\ ‰$ can be derived. We are now in a position to calculate the corresponding equations for magnesium and bicarbonate. (Table V).

Having these equations, we can calculate the composition of sea water corresponding to that in Knudsen's *Hydrographical Tables* at any chlorinity, assuming that the ratios to chlorinity of all the other components except these four are constants; an assumption which, even if incorrect, will introduce no significant discrepancy. The total salt per kilogram, Σ, as distinguished from the salinity, S, will be given by the expression, $\Sigma = 0.073 + 1.8110\ Cl\ ‰$. The total salt per kilogram of solvent water, Z, will then be $Z = 1000\ \Sigma/1000 - \Sigma$, or

$$Z = \frac{73 + 1811\ Cl\ °/_{oo}}{999.927 - 1.8110\ Cl\ °/_{oo}}.$$

This quantity Z is useful in dealing with the colligative properties of sea water, as Table VI will show. Here are given the values of Z corresponding to even units of chlorinity, the freezing point, τ, of sea water as measured by Hansen (Knudsen, 1903), and the freezing point as calculated from the equation $\tau = -0.05241\ Z$. Hansen's attempt to express freezing point as a function of another property of sea water led to a more complicated equation, namely $\tau = -0.086 - 0.064633\ \sigma_0 - 0.0001055\ \sigma_0^2$.

The ionic strength, a quantity of importance in the thermodynamics of solutions, can likewise be calculated for sea water. The ionic strength, μ, is computed by first multiplying the concentration of each individual ion, in moles per kilogram of solvent water, by the square of its valence, and then taking half the sum of these products (Lewis and Randall, 1923, p. 373). Proceeding in this way, we obtain

$$\mu = \frac{1.47 + 35.92\ Cl\ °/_{oo}}{999.927 - 1.8110\ Cl\ °/_{oo}}$$

which may also be expressed in the form $\mu = 0.00147 + 0.03592\ Cl\ ‰ + 0.000068\ (Cl\ ‰)^2$ in the range of concentrations encountered in naturally occurring sea water. This compares favorably with the equation $\mu = 0.020\ S\ ‰ = 0.036\ Cl\ ‰$ derived by Buch *et al.* (1932, p. 35) from Dittmar's original analyses.

TABLE VI

TOTAL SALTS PER KILOGRAM OF SOLVENT WATER AND FREEZING POINT

Chlorinity °/₀₀	*Z, total salts per kg.* H_2O	$\tau = -0.05241\ Z$	τ, *measured*
1	1.888	−0.099	−0.099
2	3.709	.194	.195
3	5.537	.290	.290
4	7.372	.386	.386
5	9.214	.483	.483
6	11.062	.580	.579
7	12.917	.677	.676
8	14.778	.775	.774
9	16.646	.873	.871
10	18.521	.971	.969
11	20.403	1.070	1.068
12	22.292	1.169	1.167
13	24.188	1.268	1.266
14	26.091	1.368	1.366
15	28.001	1.468	1.466
16	29.919	1.568	1.567
17	31.884	1.669	1.668
18	33.778	1.779	1.769
19	35.716	1.872	1.872
20	37.662	1.974	1.974
21	39.616	2.076	2.078
22	41.577	2.179	2.181
23	43.546	−2.283	−2.286

DISCUSSION

Since chloride determinations made with sodium or potassium chloride as a primary standard, or made gravimetrically, and calculated with the present accepted values for atomic weights, will differ slightly but measurably from determinations using Copenhagen Normal Water, it is important that the method of chloride determination be adequately described in reporting chemical oceanographic data. Variations in the reported ratios of other components to chlorinity may be caused by this ambiguity in the method used for chlorinity. Likewise the ratios must be reduced to a vacuum basis, in accordance with the definitions of salinity and chlorinity.

TABLE VII

HYPOTHETICAL COMBINATION OF IONS IN SEA WATER

$Cl = 19.00‰$

Salt	*Grams*
$NaCl$	23.477
$MgCl_2$	4.981
Na_2SO_4	3.917
$CaCl_2$	1.102
KCl	0.664
$NaHCO_3$	.192
KBr	.096
H_3BO_3	.026
$SrCl_2$	.024
NaF	.003
Sum	34.482
H_2O to	1000.000

That the ratios of other ions to chlorinity in sea water are not strictly constant follows from the relationship between chlorinity and salinity established by Knudsen. Brackish waters will vary according to the nature of the particular river water with which they are diluted. It happens that water from the Baltic region was selected as the standard type of diluted water in oceanography, and comprehensive tables of its salinity, chlorinity and density relationships worked out. It follows from this that it is not possible, by extrapolation to zero chlorinity of measurements made in natural sea water, to obtain the corresponding property of distilled water, although this has been attempted in the case of refractive index, dissociation constant, and other measurements. It is also incorrect to make electrical measurements in sea water over a range of chlorinity, by diluting a single sample with "a good grade of conductivity water," although this likewise has been done. Samples diluted with distilled water will not correspond in properties to those of water of the same chlorinity from Knudsen's Tables. Furthermore, in any specific locality where dilution by river water occurs water of a given chlorinity will not necessarily have the same properties as water of the same chlorinity obtained by diluting oceanic water with distilled water nor water corresponding to that of Knudsen's Tables.

In Table VII the ions previously presented in Table III are combined as salts. This tabulation may serve as a basic formula for synthetic sea water of chlorinity 19.00 ‰. It should be noted that as only the major constituents have been discussed the so-called plant nutrients and heavy metals are lacking.

Not only must the qualification "in oceanic water unaffected by land drainage" be added to the principle of constant composition of sea salt, but also, the depth at which the sample is obtained must be specified. The nutrient compounds, nitrate, phosphate and silicate, increase with depth to a point where they can no longer be considered infinitesimal, and the decreased pH favors increased solution of $CaCO_3$ from settling organic detritus. It was for this reason that the calcium and base ratios presented in Table III were both chosen from determinations on samples taken from the upper layers in the same area.

SUMMARY

1. Dittmar's values for the composition of the dissolved solids in sea water are recalculated with 1939 atomic weights.

2. If Copenhagen Normal Water is not available, chloride values obtained using a primary Cl standard must be converted to chlorinity. Jacobsen and Knudsen have found the chlorine-equivalent (1939 atomic weights) to be 1.00045 times chlorinity.

3. To correspond to the definitions of chlorinity and salinity, weighings should be corrected to weights *in vacuo*.

4. Modern determinations of the constituent : chlorinity ratios for surface ocean water have been adjusted as given above and compared with Dittmar's values. Since certain of these ratios increase with decreasing chlorinity, the properties of ocean water diluted with distilled water will not agree with Knudsen's Tables. Certain ratios also increase with depth.

5. From these ratios have been calculated a recipe for artificial sea water, and equations for computing total salt per kilogram of sea water, Σ; total salt per kilogram of solvent water, Z; and ionic strength, μ; in terms of chlorinity.

LITERATURE CITED

Baxter, G. P., *et al.*
1939. Ninth report of the Commission on Atomic Weights of the International Union of Chemistry. J. Am. Chem. Soc., 61, 223–228.

Buch, K., *et al.*
1932. Über das Kohlensäuresystem im Meerwasser. Conseil intern. exploration mer, Rapp. et Procès-Verbaux, 79, 1–70.

Deacon, G. E. R.
1933. An examination of "Eau de Mer normale P 13, 28–VI–1929." With appendix by D. J. Matthews. J. conseil intern. exploration mer. 8. 59–63.

Desgrez, A., and Meunier, J.

1926. Recherche et dosage du strontium dans l'eau de mer. Compt. rend., 183, 689–691.

Dittmar, W.

1884. Report on researches into the composition of ocean water, collected by H. M. S. *Challenger,* during the years 1873–1876. Voy. *Challenger,* Physics and Chemistry, 1 (1), pp. 1–251.

Gripenberg, S.

1937. The calcium content of Baltic water. J. conseil intern. exploration mer, 12, 293–304.

Harding, M. W., and Moberg, E. G.

1933. Determination and quantity of boron in sea water. Proc. Pacific Sci. Congr., 5th Congr., Can., 3, 2093–2095.

Igelsrud, I., Thompson, T. G., and Zwicker, B. M. G.

1938. The boron content of sea water and of marine organisms. Am. J. Sci., 35, 47–63.

Jacobsen, J. P., and Knudsen, M.

1940. Urnormal 1937 or primary standard sea-water 1937. Assoc. Oceanogr. Physique, Pub. Sci. No. 7, Liverpool. 38 pp.

Kirk, P. L. and Moberg, E. G.

1933. Microdetermination of calcium in sea water. Ind. Eng. Chem. Anal. Ed., 5, 95–97.

Knudsen, M.

1901. Hydrographical Tables. Copenhagen. 63 pp.

1902. Berichte über die Konstantenbestimungen zur aufstellung der Hydrographischen Tabellen. K. Danske Videnskab. Selsk., Skrifter, Naturvidensk, math. Afdel 6, Part 12, No. 1, 151 pp.

1903. Gefrierpunkttabelle fuer Meerwasser. Conseil intern. exploration mer, Pub. circ. No. 5, pp. 11–13.

Lewis, G. N., and Randall, M.

1923. Thermodynamics and the free energy of chemical substances. New York. 653 pp.

Mitchell, P. H., and Solinger, J. L.

1934. The effects of land drainage upon the excess bases of sea water. Biol. Bull. 66, 97–101.

Miyake, Y.

1939. Chemical studies of the western Pacific Ocean I and II. The chemical composition of the oceanic salt, parts 1 and 2. Bull. Chem. Soc. Japan, 14, 29–35 and 55–58.

Revelle, R. R.

1936. Marine bottom samples collected in the Pacific Ocean by the *Carnegie* on its 7th cruise. Scripps Inst. Oceanog. Univ. Calif., Dissertation.

Thomas, B. D., and Thompson, T. G.

1932. (Determination of strontium in sea water.) Cited by Thompson and Robinson, 1932, p. 174.

Thompson, T. G., Johnston, W. R., and Wirth, H. E.

1931. The sulfate-chlorinity ratio in ocean waters. J. conseil intern. exploration mer, 6, 246–251.

Thompson, T. G., and Robinson, R. J.

1932. Chemistry of the sea. Bull. Nat. Research Council, No. 85, pp. 95–203.

Thompson, T. G., and Taylor, H. J.

1933. Determination and occurrence of fluorides in sea water. Ind. Eng. Chem. Anal. Ed. 5, 87–89.

Thompson, T. G., and Wirth, H. E.

1931. The specific gravity of sea water at zero degrees in relation to the chlorinity. J. conseil intern. exploration mer, 6, 232–240.

Thompson, T. G., and Wright, C. C.

1930. Ionic ratios of the waters of the north Pacific Ocean. J. Am. Chem. Soc., 52, 915–921.

Webb, D. A.

1938. Strontium in sea water and its effect on calcium determinations. Nature, 142, 751–752.

1939. The sodium and potassium content of sea water. J. Exp. Biol., 16, 178–183.

Wentworth, C. K.

1939. The specific gravity of sea water and the Ghyben-Herzberg ratio at Honolulu. Univ. Hawaii Occasional Papers No. 39, Univ. Hawaii Bull., 18 (8), 24 pp.

Contribution No. 94

(Reprinted in U. S. A. from Transactions of 1940 of the American Geophysical Union)

RESEARCH WITHIN PHYSICAL OCEANOGRAPHY AND SUBMARINE GEOLOGY AT THE SCRIPPS INSTITUTION OF OCEANOGRAPHY DURING APRIL 1939 TO APRIL 1940

H. U. Sverdrup

(Contribution from the Scripps Institution of Oceanography, New Series, No. 94)

Emphasis will again be placed on the activities within the fields of submarine geology and ysical and chemical oceanography, although researches within the biological fields cover the eater part of the work at the Scripps Institution of Oceanography. The compilation and dis- ssions of field-data and the studies in the laboratory have been greatly facilitated by assis- nce obtained from the Works Progress Administration Project No. 665-07-3-141.

As previously, the sediments-laboratory has made a large number of mechanical and partial emical analyses of sediment-samples in the collections of the Scripps Institution. In approx- ately 50 cores collected on the 1939 cruise of the vessel E. W. Scripps to the Gulf of Cali- rnia the particle-size distribution and contents of calcium carbonate, organic nitrogen, water, d chloride have been determined at a series of ten or more depths within each core. Likewise, presentative portions of the sediment-samples collected in 1938 under the direction of F. P. epard have been analyzed, together with cores collected during the present year off the Lower lifornia coast and in southern California waters by Revelle. The analytical work has been pported in part by a grant from the Geological Society of America and by other funds from out- de sources, while the making of such a large number of analyses has been possibly only because technical assistance supplied by the Works Progress Administration.

Besides the above studies of the relationships between certain sedimentary characteristics d environments of deposition, considerable attention has been directed during the past year to vestigation of sedimentary processes, particularly to problems of transportation of debris in e sea and to physical and biochemical processes in sediments after deposition.

Problems of sediment-transportation may be conveniently divided into two categories, name- the nature of transporting agencies, and the character of transported materials. In collab- ation with Carl Johnson, a tripod has been developed containing three Ekman-type current-meters ranged one above the other, by which it has proved possible to measure the vertical distribu- on of velocity within a meter of the sea-bottom in waters of considerable depth, without horing the ship. Six series of measurements for periods greater than 12 hours have been made a variety of environments, including offshore banks, the mainland shelf, and the deep Santa ica and Santa Cruz basins. An unexpected feature of the results was the observation of ve- ities up to 15 cm/sec at the bottom of the Santa Cruz Basin in waters 1,900 meters deep and rly 1,000 meters below the sill depth of the Basin.

With the aid of a grant of funds from the American Association of Petroleum Geologists, dies of the character of transported materials are being carried out by means of sediment-

traps near the bottom. The relative efficiency of different types of traps in capturing the sedimentary load of moving waters is being investigated as a fundamental part of this work, which is being carried on in collaboration with F. P. Shepard and K. O. Emery. In the laboratory, studies of the process of coagulation of colloidal suspended materials by salts in sea-water have been made in cooperation with Mrs. Lois Sorkness. It has been found that the degree of coagulation varies directly with the concentration of suspended material, as well as with the concentration of dissolved salts.

Problems of physico-chemical and biological equilibria in marine muds have likewise been approached from several different aspects. Investigations of the distribution and activities of aerobic and anaerobic bacteria in cores have been made by S. Rittenberg, who has also measured by means of a glass electrode the vertical distribution of pH in freshly-collected cores of various types. Relative high pH-values, well over 9.3, have been observed in calcareous cores at depths of 100 or more centimeters beneath the surface, while values as low as 7.4 have been found in highly organic sediments. An attempt has been made to determine the amounts of iron sulfide in muds of different environments, but in only a few cases have determinable quantities been detected, even where H_2S was obviously present. In connection with studies of the sulfur cycle in marine muds a conductiometric titration-method for the determination of sulfate, chloride, and other dissolved salts in sea-water and in interstitial waters of marine sediments has been developed, chiefly by L. J. Anderson.

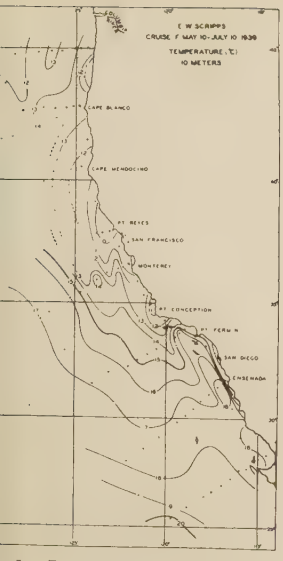
E. C. La Fond has had supervision of an instrument for recording wave-heights and periods and of a current-meter, both at the end of the Institution's pier, and has obtained daily record whenever weather-conditions permitted. He has taken soundings and other observations on the beach weekly at the Scripps Institution pier, the Del Mar pier, and Crystal pier, the number of soundings totaling about ten thousand.

Owing to greatly reduced clerical help, averaging and plotting by months and quadrangles of sea-surface temperatures reported to the Scripps Institution by navigators of steamers in the Pacific Ocean continued only till August, 1939.

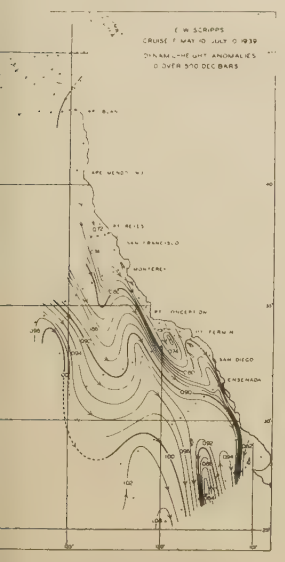
The Works Progress Administration project, sponsored in 1935 by the University of California for compiling oceanographic data reported by navigators of all ships in the Pacific to the United States Hydrographic Office from 1904 through 1934, was completed late in the summer of 1939. All of the coding sheets (about 60,000), containing data from the Pacific Ocean, are now on file at the Scripps Institution for use in studies of ocean-surface conditions--in particular, the seasonal and yearly variations of surface-currents in the Pacific Coastal region of California. Progress in compilations begun in August, 1938, from the coded sheets to forms designed for the above studies was interrupted in August, 1939, because of reduced clerical help.

Because of continued interest evidenced by correspondence with many individuals and representatives of various organizations, the usual work of providing advance indications of air- and sea-temperatures and seasonal precipitation of Pacific coastal areas was done. As usual, advance indications were mimeographed in October for our mailing list and for the press. Mr. Gordon has made some progress in revising his preliminary approach to problems of rainfall-cycles. The improvement involves random variations in phases which, for predicting, has the advantage over the ordinary Fourier development that the quantities are given directly in terms of observations up to the time of prediction. The United States Department of Agriculture has continued for several years a critical examination of various long-range forecasting methods in use and has carried on special investigations of the forecasting problem. Quite properly a Government agency should ultimately provide such forecasts. Long-range forecasts even approximating to the high standard being realized in those for short periods necessarily involve world-wide observations and solutions of various complicated meteorological problems. Their realization requires an extensive cooperative undertaking and no agency is better equipped for this than the Weather Bureau. Meanwhile, even the very meager service now being rendered by other agencies will likely continue in response to immediate requirements.

Since November, 1939, when the Polish climatologist, Dr. W. Gorczynski, began working at the Scripps Institution on his studies of comparative climates of California and other Western States with sunny regions of Europe and Africa, most of the time and facilities of one division have been devoted to his climatic studies. This has involved a large amount of compilation and computing and the preparation of many charts at a time of great reductions in clerical and other help. McEwen has collaborated in these climatic studies and has worked out certain technical problems of a statistical nature whose solution was needed. In particular, these problems have been concerned with erros and standardization of the precipitation-ratio, and will be prepared for publication. Among various proposed publications based upon Dr. Gorczynski's climatic in-



1--Temperature-distribu-
on off coast of California
depth of 10 meters, ac-
ding to observations May
to July 10, 1939



2--Dynamic topography of
-surface off coast of
ifornia relative to 500-
ibar surface, according
bservations May 10 to
10, 1939

vestigations is a somewhat popular small book on "California's sunny climates."

While not bearing directly on oceanography or the problem of long-range forecasting, this investigation involves the "field" rather than the laboratory point of view and should be a valuable supplementary undertaking.

In order to facilitate numerical applications of statistical methods that he has devised and published for estimating the densities of bacterial populations in solutions, Mr. Gordon has prepared a five-page paper entitled "A shorter method of computation of the estimate of the mean and variance," which will serve until appropriate tables have been computed.

A problem arising in McEwen's formula for computing surface-currents from temperature, referred to in the report of 1939, of estimating the error of a quotient, has been worked out by Mr. Gordon. Extensive applications of the formula have been made to North Pacific Observations and the results are being assembled for publication.

Computations of turbulence and vertical velocity have been made from numerous sets of serial temperatures and salinity-observations within ten miles of La Jolla and at various months within a ten-year period. Methods of computation developed earlier were used.

Mr. Gordon, as a result of studying an earlier (1929) publication of McEwen's on a theory of the vertical distribution of properties in a body of water, has made further progress in developing a more fundamental method, using a turbulence-coefficient varying with the depth and assuming that energy is dissipated at a rate proportional to this coefficient. His results do not seem too complicated for numerical application to ocean-observations.

Methods developed earlier have been applied to various types of problems involving the dispersion in three dimensions of suspended material concentrated near shores and settling at a constant rate.

E. G. Moberg and his assistants have devoted much time to routine work in connection with the cruises of the E. W. Scripps. During the past year several hundred water-samples have been analyzed for calcium. These comprise samples from the Gulf of California, from the local areas which are now being investigated, from the long summer cruise of 1939, and from the Bushnell stations between San Diego and Panama. The results of all these analyses are now being studied. Whether they will be worth reporting upon is yet to be decided.

On the cruises in progress the distribution of phosphates is being examined at various depths and promising results are accumulating. The nitrogen in all bottom-samples obtained in the Gulf of California has been determined and these analyses have produced significant results. John Lyman is engaged in experimental work bearing on the carbon-dioxide equilibrium in sea-water.

The data from the cruise to the Gulf of California between February 5 and March 31, 1939, h was mentioned in last year's report, have been compiled by H. U. Sverdrup and R. H. Flem- and a discussion of the major features of the physical and chemical characteristics of the rs of the Gulf was presented at the meeting of the International Association of Physical nography in September, 1939.

Between May 10 and July 10, 1939, a cruise off the California coast was made in cooperation the Federal Bureau of Fisheries. On the cruise 77 stations were occupied, most of them

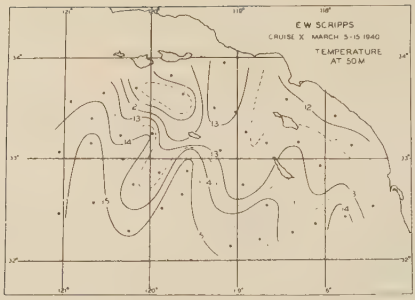


Fig. 3--Temperature-distribution off southern California at depth of 50 meters, according to observations March 5 to 15, 1940

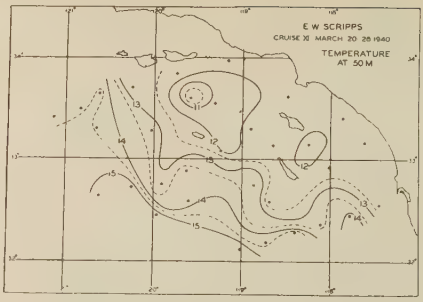


Fig. 4--Temperature-distribution off southern California at depth of 50 meters, according to observations March 20 to 28, 1940

lying along six lines extending from points on the coast betwen latitudes 45° north and 25° north to distances of 300 to 350 miles from the coast. Unfavorable weather prevented work off the coast between Point Reyes and Cape Mendocino. Figures 1 and 2 show the distribution of temperature at a depth of ten meters and the topography of the surface relative to the 500-deciba surface. The distribution of temperature clearly demonstrates the effect of upwelling and also shows a tongue-like distribution of temperature off southern California similar to the one which was observed on cruises in that area in 1937 and 1938. The chart of the topography of the surface demonstrates the character of the California Current and the existence of the previously observed eddy off the coast of southern California. The character of the water-masses along the southern lines of stations off Cedros Island (latitude 28°) indicates a transition to the subtropical waters of the Pacific. It is probable that shortly south of this latitude the current turns west and joins the north equatorial current across the Pacific Ocean. The working up of the data of the cruises has been conducted by Richard Tibby. After a cruise in August, 1939, on which cores of sediments were procured and current-measurements near the bottom were undertaken, the E. W. Scripps was laid up until the end of February, 1940. Necessary work of maintenance was completed including installation of new batteries and change of the bow.

On March 5, 1940, the E. W. Scripps left for the first of a series of cruises, again in cooperation with the Federal Bureau of Fisheries. On these cruises a small area off southern California will be examined in detail. Up to 40 stations will be occupied on each cruise if weather conditions permit, each cruise lasting ten to twelve days. After a few days in port the same stations will be reoccupied and it is expected that at least six cruises will be made during March, April, May, and the first half of June. By means of the data obtained on the consecutive cruises it is hoped that it will be possible to derive the trajectories of individual water-masses and study the changes in populations which occur within such water-masses. Figures 3 and 4 show the temperature-distribution at a depth of 50 meters on the first two cruises which were completed between March 5 and 15 and March 20 and April 5, respectively. The similarity of the two pictures is striking but certain systematic differences can be seen indicating that the density of the network of stations and the short time-interval between cruises will make possible the hoped-for analysis. The compilation of the data is in progress under the supervision of R. H. Fleming. The calculations of specific volumes and dynamic heights are greatly facilitated by new tables which have been prepared by E. C. La Fond.

A new series of publications from the Scripps Institution has been established under the title "Records of observations, Scripps Institution of Oceanography." The first number of this new series will appear shortly and will contain the oceanographic observations made on the six cruises of 1938 with preliminary discussions. It will also contain a complete description of the research-vessel E. W. Scripps of the Institution. The second number will contain the oceanographic observations which were made in 1939, but the preparation of the manuscript has been delayed owing to a temporary interruption of the assistance rendered by the Works Progress Administration. The new series will be printed in offset by the University of California Press.

Scripps Institution of Oceanography,
University of California,
La Jolla, California

Contribution No. 95

Contributions from the Scripps
Institution of Oceanography
New Series, No. 95

TRAIL BLAZING IN THE PACIFIC

RESEARCH IN OCEANOGRAPHY

CALIFORNIA SCIENTISTS STUDY THE OCEAN

BY DR. H. U. SVERDRUP

DIRECTOR OF SCRIPPS INSTITUTION OF
OCEANOGRAPHY

Reprinted from California Monthly *for December, 1940*

NEARLY thirty years ago, when I held my first job as a research assistant, I knew that there was nothing I should like better than to continue in scientific work. However, I had certain misgivings as to my ability and turned to my professor for advice. He told me that he could not as yet express any opinion as to my qualifications, but he added, "I can tell you this. Scientific work is the easiest you can select." When I looked surprised he explained, "Because in research you have only to deal with problems which you formulate yourself, but in all other occupations you will have to deal with human beings, and that is much more difficult than dealing with nature."

At that time I did not fully understand his meaning, but if we look back on the development of our civilization it is not hard to realize how correct the observation was. During the last century, thanks to scientific research and application of science to technical problems, we have attained an undreamed-of mastery of our surroundings and of natural resources, but man himself has no greater control over his emotions and reactions than he had thousands of years ago. The present conditions, when the highest technical skill is used for purposes of destruction, bear horrible evidence to the difficulties encountered in dealing with human beings as contrasted with the simplicity of research.

One may well ask if it is worth while to continue scientific research in view of the fact that the results are applied as much to destruction as to construction—an application which is characteristic not alone of our period but which has been true as long as technical advances have been made. The story goes that when Galileo demonstrated his telescope to the rulers of Venice hoping that at the first sight of the moons of Jupiter they would share his enthusiasm, their comment was, "What a marvelous instrument this will be in time of war when you can use it for spying on the advancing enemy."

Similarly, every achievement of science has been applied whenever possible for purposes of war, wherefore the question, "Is it worth while to continue research as long as man destroys values as fast as they accumulate?" This present time is not one in which it is easy to be an optimist but I, for one, refuse to be a pessimist and I refuse to believe that the results of scientific endeavor have been of no value to man at all, no matter how misused many of these achievements have been. It must be admitted that much greater efforts should be directed towards the understanding of man and his reactions, the functioning of society, and the underlying reasons for the numerous conflicts of interest, but scientific research dealing with the surrounding nature should hold its own.

As I see it, the motive for all these efforts, those directed towards the understanding of man and those directed towards the understanding of nature, is our search for *security,* because we are all intimately concerned about our own security and that of the coming generation. Educational institutions have been created in order to fit the coming generation for its place in society, hospitals have been built and medical services are rendered for safeguarding every one of us, the delicate machinery of the law has been developed for the protection of the majority of the citizens. Going on, we find that the desire for security for ourselves and our children dictates a wide range of our activities, and that even wars are waged for the purpose of securing the future of countries. In this latter and in many other cases the means employed for achieving security appear to defeat their own purpose, but that purpose remains the same.

If we consider security as one of the outstanding goals of all our efforts, research within the fields of natural sciences has indeed a place. The aims of such research should be, partly, to make us familiar with the world in which we live by contributing to our understanding of the events in the surrounding nature, and partly, to build a foundation for economic use of natural resources. The latter aim often receives too great an emphasis, perhaps because the results in physics, chemistry, general biology, medicine, and other natural sciences have led to such a number of notable technical advances with bearing on household problems that often it is taken for granted that in these fields research must necessarily lead to practical results if it shall be worthy of support.

There is one notable exception: astromony. The sun, the moon, and the stars have always fascinated men who, since time immemorial, have speculated over the riddles of the sky and to whom the answers to their questions have been ample reward for their support of astronomical research, although these answers have not contributed in the least towards making life easier or more convenient. They have, however, contributed to the feeling of security based on knowledge and they have removed much of the fear of the unknown.

When mentioning fascinating fields of research, I venture to place oceanography in conjunction with astronomy. It appears permissible to do so here where we live on the shores bordering the largest ocean on earth, an ocean less charted than the surface of the moon, the currents of which are less known than the orbits of stray comets. It is an ocean in which myriads of organisms compete for existence, in which are found survivors of forms present in the oldest geological strata, and in which the history of our planet is today being written in layers of silt and clay which will rise as new

ıountain ranges in ages to come. With the excep-
on of a thin surface layer, the ocean is a world
f black darkness as contrasted with our sunny
ırroundings, a world in which the strange crea-
ıres of the abysmal depths carry their own pecu-
ar lanterns and in which life is found under con-
itions we can hardly realize.

The study of the world is worth undertaking
ecause the knowledge of the character of the
cean currents and of their changes, of the distri-
ution of plants and animals of the sea and of
ieir complicated interrelationships, will give us
ie satisfaction of a better understanding of this
ırth of ours. I believe that such studies as those
hich, at the Scripps Institution of Oceanography,
ere initiated thanks to the generosity of E. W.
nd Ellen B. Scripps, and which have received
ntinued support by the Scripps family, represent
ı activity worthy of the University of California.
hope that for a long future the University can
ntinue active exploration of the ocean which
ashes against California's extended coast. Let me
iefly review the equipment of the Scripps Insti-
ıtion for its task and present my views as to the
est manner in which the Institution can serve.

Our laboratories are well supplied, our library
adequate for our purposes, our vessel is a staunch
nd seaworthy craft suited for making observations
nd collections at sea, and on our staff we have a
umber of specialists working in apparently wide-
separated fields. Some study the physics of the
cean, the types of currents and their changes, or
e interaction between the atmosphere and the
cean; others study the chemistry of the sea water,
cluding the amounts of the very important plant
ıtrient salts, such as phosphates and nitrates;
hers examine the minute floating plants, the
ıytoplankton, of the sea; others, the numerous
nall animals, the zooplankton. Some deal with
e bacteria of the sea which are of an importance
mparable to that of the soil bacteria, others
ain are working on problems related to the bio-
emistry of the marine organisms or to the physi-
ogy of fishes; and finally, still others are engaged
studies of the ocean bottom, its topography, the
pes of sediments which are being laid down, and
e processes of sedimentation. This sounds like
enumeration of unrelated subjects, but they
deal with some phase of oceanography.

It has been my hope, since I became acquainted
th the Scripps Institution, to place emphasis on
ıat all the special fields have in common—the
ean itself—in order to develop a program for
e Institution as such, in which as many as pos-
ıle of our specialists can participate. In this man-
r results in one field may find application in
other and more rapid advances may be expected.
The possibility for greater collaboration be-
tween the specialists here presented itself when the late Mr. R. P. Scripps in 1937 gave us our new research vessel. At that time we had the choice between two lines of attack, a general exploration of some of the many large unknown areas of the Pacific Ocean, or an intensive study of a small area within easy reach.

A general exploration had several tempting aspects. A large triangle of the Pacific Ocean extending from between San Diego and Peru with its apex at the Hawaiian Islands, covering an area larger than half of the North Atlantic Ocean, is completely unknown from the oceanographic point of view, and expeditions over a period of years for an examination of this area would be more exciting and might attract wider attention than the repeated studies within a small region. The disadvantage of a program of this nature would be that emphasis would have to be placed upon what the conditions are, and the question of *why* such conditions exist and why they are subject to change could not be approached. It is of greater interest, however, to examine why certain changes take place than to confine oneself to establishment of what is present. It was therefore decided to follow the second line of attack and to undertake intensive work in a small area, which also offers the advantage that in this type of work more direct coöperation between the divisions at the Institution could be established than would be possible when conducting general surveys.

During the years of 1938 and 1939 our work at sea was of a preliminary character. By making repeated cruises off the coast of southern California in 1938 and by completing in 1939 a long cruise extending from the Oregon border to Cedros Island off Lower California, we have obtained fairly good knowledge of the character of the waters, the types of currents, the dominating populations, and the more outstanding annual changes within the sea off these coasts. We have not quite been able, however, to resist the temptation of thrilling exploratory work, and in the spring of 1939 we made a cruise to the Gulf of California, from which the first picture of the character of the water masses in the Gulf resulted, and on which it was found that the Gulf represents a model area for the study of present processes of sedimentation. We hope to make other cruises to the Gulf on which intensive and systematic work in submarine geology shall be conducted, but our plans are still under development and instead of discussing them I shall return to our work off this coast.

Last winter we felt that we had sufficient preliminary information to plan more intensive work. Accordingly, during the past spring, between March 5 and June 8, we have completed in rapid succession six cruises, each covering an area be-

tween San Diego and the Channel Islands, and extending to a distance of about 140 miles from the coast. We have secured a series of consecutive pictures of the currents and water masses within the selected area and also of the characteristic population of microscopic plants and smaller animals. By comparing these pictures from cruise to cruise we shall be able to follow the changes which took place, and if our data are adequate we may be able to approach the question of why changes occur.

It is evident that an enterprise of this nature requires the complete coöperation of a number of specialists. The physical oceanographer has to account for the character of the currents and has to examine why the observed patterns exist. The chemist has to determine the salinity and oxygen content of the water and to pay particular attention to the small amounts of nutrient salts which are of the utmost importance to the development of the tiny floating plants. The marine botanist has to determine the number and character of plants present, the zoologist has to study the populations of animals which graze on the microscopic plants, and together the two latter have to enter upon the question of interrelationships between the different groups of organisms. The bacteriologist has to provide the answers to a number of questions dealing with the decomposition of organic matter, and in course of this work the specialists in each line have to turn to all the others in order to obtain as complete information as possible as to the events which take place.

We do not yet know whether the results of last spring's cruises will be up to our expectations, but in our preliminary work we have already arrived at some gratifying results which illustrate the value of coöperation. As an example, I may mention that in 1938 we were able to show that eddies of coastal water were often detached and carried by the general current towards the south and out to considerable distances from the coast. These conclusions were based entirely upon the examination of the physical-chemical characteristics of the waters. When examining the samples of zooplankton, one of our zoologists studied the distribution of larvae of the common sand crab, the adult species of which live on sandy beaches, and he found such larvae at distances up to 150 miles from the coast. When plotting the localities where these larvae occurred it turned out that all catches were made within eddies of coastal water. The dispersal of these larvae which, when carried out to sea, were doomed to die would have been a mystery without knowledge of the currents but was satisfactorily explained because the existence of these detached eddies had been demonstrated independently. Sim ilarly, it has been possible to show that a close re lationship exists between the number of floatin plants in the surface layers and the physical-chem cal characteristics of the surface waters, a relatior ship which we hope to follow more closely on th cruises which are now in progress. I may also ad that the preliminary work in submarine geolog in the Gulf of California gave such promising re sults because the findings could be interpreted b means of simultaneously obtained information a to the character of the water, the populations i the surface layers, and the activity of bacteria i the bottom mud. These few examples serve t emphasize the unity of the marine sciences an the necessity of complete information in order t arrive at an understanding of what happens an why.

I have dealt particularly with the work at se but I do not wish to leave the impression that th work should be considered of greater importanc than experimental studies in the laboratory. Th latter have to be conducted parallel with the wor at sea and have to assist us in the interpretatio of conditions in the ocean. When dealing with th physics of the ocean we have to make use of resul in theoretical hydrodynamics or of laws which ar based on experiments in fluid mechanics. Similarl it is necessary in biological research to base nume ous interpretations on the results of controlled ex periments during which the effects of single factor have been studied.

Let me in conclusion return to the question o the purpose of such research as is conducted here I have emphasized that the striving for the unde standing of nature is an object of equal importanc with the accumulation of knowledge applicable t economic problems. In my opinion, the task of th Institution is to promote the understanding of th events which occur in the ocean, and to place wha ever advances are made at the disposal of thos who wish an answer to a question which has inte ested them or of those who can use the added in formation to facilitate any kind of economic ente prise. We are particularly pleased if we can assi in the solution of practical problems, we are i close coöperation with a number of organizatior which are directly concerned with such matter and we hope that as our program advances we sha be in better and better position to give sound ad vice. We have no greater pleasure than answerin questions if we are able to do so, but far too ofte we find that we do not yet know the elements o oceanography and that we are only crossing th threshold to a big and fascinating world.

Contribution No. 96

In
New Series, No. 96

Reprinted from Biological Bulletin, Vol. LXXVIII, No. 3, 388–402, June, 1940
Printed in U. S. A.

SOME FACTORS WHICH INFLUENCE OXYGEN CONSUMPTION BY BACTERIA IN LAKE WATER[1]

CLAUDE E. ZOBELL[2]

(From the Limnological Laboratory and the Department of Agricultural Bacteriology, University of Wisconsin)

The conditions which influence the distribution of oxygen in lake water are the subject of an extensive literature (Thienemann, 1928; Grote, 1934), but there is relatively little information on the rôle played by bacteria regardless of the alleged importance of these organisms as agencies which deplete the oxygen content of natural waters. Birge and Juday (1911) state that the respiration of the bacteria of decay is more important than the respiration of aquatic animals in the utilization of oxygen. According to Domogalla, Fred and Peterson (1926) the oxygen content of lake water below the photosynthetic zone is inversely proportional to the abundance of bacteria. Similarly, Kusnetzow and Karsinkin (1931) report that the zones of diminished oxygen tension in Lake Glubokoje are caused primarily by bacterial activity. Seiwell and Seiwell (1938) attribute the oxygen minimum layer in the sea to the increased decomposition of organic matter by bacteria in such zones. Pütter (1924) expresses the view that bacteria consume more oxygen in sea water than all other organisms combined.

Some workers have assumed erroneously that the amount of oxygen consumed by bacteria in water can be evaluated merely by storing samples of raw water in the dark in glass-stoppered bottles and determining the oxygen content after different periods of incubation at the *in situ* temperature. This procedure may serve to estimate the amount of materials in such water which can be oxidized by bacteria but it fails to indicate the rate or the amount of oxygen consumption *in situ* because the storage of water in the laboratory is always accompanied by increased and altered bacterial activity (ZoBell and Anderson, 1936). Therefore, in order to ascertain how much oxygen is consumed by bacteria in lakes, several factors which influence oxygen consumption must be considered.

[1] This investigation was supported by grants from the Brittingham Trust Fund and the Wisconsin Alumni Research Foundation. Part of the cost of technical assistance was defrayed by the Works Progress Administration.

[2] Visiting investigator on sabbatical leave from the Scripps Institution of Oceanography, University of California, La Jolla.

Influence of Temperature

Water temperatures ranging from 0° to 35° C. or higher occur in lakes. In order to evaluate the effect of temperature upon the rate at which bacteria consume oxygen, the following experiments were conducted. Water was collected from Lake Mendota in 5-gallon carboys and thoroughly shaken to insure uniformity of its bacterial and chemical composition. It was then siphoned into each of several dozen 145 ml. oxygen bottles. The latter were divided into four lots and transferred to water baths held at 8°, 18°, 25° and 37° C. respectively. Duplicate bottles from each lot were analyzed for the oxygen content of the water by the Winkler method at the beginning of the experiment and after different periods of incubation. In most cases duplicate determinations agreed to within 0.03 mgm./l. and additional bottles were analyzed if the divergence of duplicates exceeded 0.10 mgm./l. The bottles were incubated in the dark to prevent photosynthetic activity. Table I shows the amount of oxygen which was consumed by the bacteria after different periods of incubation.

TABLE I

Amount of oxygen consumed by bacteria in Lake Mendota water incubated at different temperatures. The water initially contained 9000 bacteria per ml. and 7.46 mgm. of oxygen per liter.

Incubation temperature	Milligrams of oxygen consumed per liter after				
	2 days	5 days	10 days	20 days	30 days
8° ± 0.3° C.	0.09	0.26	0.61	1.32	2.84
18° ± 0.3° C.	0.31	1.43	2.41	3.06	3.77
25° ± 0.1° C.	0.56	2.02	2.37	3.95	4.49
37° ± 0.2° C.	0.49	1.84	2.95	4.11	4.76

A multiplicity of correlative factors are involved in the interpretation of the results. In the first place it must be recognized that the rate of reproduction and the death rate of bacteria as well as their respiratory rate are influenced by the temperature of the water. During the first 24 hours the bacterial population of the water incubated at 8° C. had trebled while that incubated at 25° C. had increased nearly a hundredfold. The bacterial population of the water incubated at 25° C. reached its maximum on the third day after which it decreased. The bacterial population of the water incubated at 18° C. reached its maximum on the fourth day and then decreased. The bacterial population of the water incubated at 8° C. was still increasing after ten days at which time

it contained more bacteria than the water incubated at the higher temperatures.

The residual organic matter becomes more and more refractory to oxidation as the more oxidizable fractions are oxidized and finally a lack of oxidizable matter limits further oxygen consumption. Although six times as much oxygen was consumed by multiplying cultures in two days at 25° C. as at 8° C., there was virtually no difference after sixty days because at all temperatures most of the readily oxidizable organic matter had been oxidized. By applying the formula of Buchanan and Fulmer (1930):

$$m = \frac{2.303\, S \log b/B}{t(b - B)}$$

where m is the oxygen consumed per cell in time t; S the total amount of oxygen consumed in time t; B the number of bacteria at the beginning of the experiment and b the number after time t; it was found that during the first 24-hour period of incubation at 25° C. the bacteria in Lake Mendota water consumed 21 to 43×10^{-12} mgm. of oxygen per cell per hour. Although the bacterial population continued to increase throughout the second 24-hour period, the oxidizable organic matter content of the water was diminished to such an extent that the bacteria used only 5.4×10^{-12} mgm. of oxygen per cell per hour. After 5 days the bacteria incubated in water at 25° C. were using only 0.5×10^{-12} mgm. of oxygen per cell per hour. During the first 24-hour period of incubation at 8°, 18°, 25° and 37° C., the bacteria consumed an average of 9×10^{-12}, 20×10^{-12}, 32×10^{-12} and 61×10^{-12} mgm. of oxygen per cell per hour respectively. Bacteria from Lake Glubokoje were found by Liagina and Kusnetzow (1937) to consume an average of 18.8×10^{-12} mgm. of oxygen per cell per hour at 10° C. and 30.3×10^{-12} mgm. at 15° C.

The influence of temperature upon the rate of bacterial respiration independent of its effect on bacterial multiplication and other variables mentioned above was investigated by inoculating lake water enriched with 0.01 per cent each of glucose and asparagine with about a hundred million bacteria per ml. The inoculant was prepared by washing the actively multiplying colonies from several bottles of nutrient agar previously inoculated with the mixed microflora from Lake Mendota and incubated at 18° C. Under these conditions the rate of oxygen consumption was found to increase exponentially with the temperature with one exception as shown by Fig. 1. The Q_{10} from 8° to 25° C. was found to be 2.1. The decelerating rate of respiration in the water incubated at 37° C. is attributed to the inactivation of some of the

thermo-sensitive bacteria or their enzymes and is not due to a lack of either oxidant or oxygen. According to Edwards and Rettger (1937) the respiratory enzymes of bacteria are especially thermo-sensitive, many being destroyed at relatively low temperatures. Similarly ZoBell and Conn (1940) have shown that prolonged exposure to temperatures exceeding 25° C. is injurious to many water bacteria and that the respiratory enzymes of some are destroyed in 10 minutes at 30° C.

Influence of Oxygen Tension

According to Amberson (1928) the rate of oxygen consumption by unicellular organisms is independent of the oxygen tension over a wide

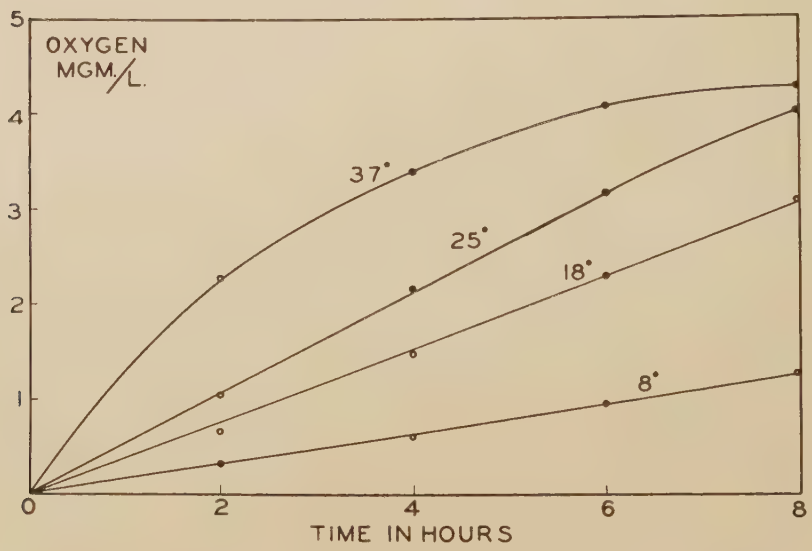


Fig. 1. Oxygen consumed after different periods of time at 8°, 18°, 25° and 37° C. by lake bacteria (resting cells) in lake water enriched with 0.01 per cent each of glucose and asparagine.

range. Similarly Pütter (1924), Harvey (1928), Pomeroy (1938) and others report that the rate of oxygen uptake by bacteria is not influenced by the oxygen tension. However, Waksman and Carey (1935), Heukelekian (1936), Schlayer (1936) and others find that the rate of oxygen consumption by certain bacteria is proportional to the oxygen tension. These antithetical observations may be due to variations in experimental procedure. For example, Kempner (1937) finds that at relatively low temperatures or with old cells the respiration of *Escherichia coli* is independent of the oxygen tension, but when using

heavy suspensions of young cells at their optimum temperature, the oxygen uptake of *E. coli* is a function of the oxygen tension. These observations suggest that all of the oxygen may be consumed in the immediate vicinity of groups or clumps of young cells more rapidly than it can reach them by diffusion. Clifton and Logan (1939) and others have shown that young cells consume oxygen much faster than old ones. According to Waksman and Renn (1936) the effect of oxygen tension is most pronounced when resistant materials are being oxidized.

The following experiments were performed to ascertain what effect the oxygen tension has upon the respiration of bacteria in lake water. The oxygen content of water recently collected from Lake Mendota was adjusted by bubbling either nitrogen or oxygen through it until otherwise identical lots of the water contained from 0.31 to 8.26 mgm./l. This was siphoned into oxygen bottles and the oxygen tension of the water was determined after different periods of incubation at 25° C. The results of the experiment, which are summarized in Table II, show

TABLE II

Oxygen consumed by multiplying bacteria in Lake Mendota water containing different concentrations of dissolved oxygen after different periods of incubation at 25° C.

Initial dissolved oxygen	Oxygen consumed after				
	1 day	2 days	3 days	5 days	10 days
mgm./l.	*mgm./l.*	*mgm./l.*	*mgm./l.*	*mgm./l.*	*mgm./l.*
0.31	0.21	0.29	—	—	—
0.85	0.23	0.41	0.54	0.79	—
1.78	0.28	0.46	0.61	0.95	1.39
4.02	0.27	0.39	0.50	0.92	1.32
8.26	0.28	0.42	0.56	1.06	1.52

that within the limits of experimental error the oxygen tension of the water does not influence the rate at which oxygen is consumed by respiring bacteria.

In several other experiments which have been reported in detail by ZoBell and Stadler (1940*a*), it was similarly found that the respiration of "resting" cells in enriched lake water as well as cultures of bacteria is independent of the oxygen tension over a wide range. Although there is a slight tendency for the oxygen tension of lake water to influence the multiplication of bacteria, there is no evidence to indicate that the oxygen uptake of bacteria is influenced by the oxygen tension until

the oxygen content is as low as 0.3 mgm./1. Even when the water was supersaturated with oxygen (as much as 26.48 mgm./1.), bacteria consumed oxygen no more rapidly than when the water contained only 0.3 mgm./1. As the oxygen tension is reduced below 0.3 mgm./1. the rate of bacterial respiration decreases rapidly.

Influence of Organic Matter

According to Friedlein (1928) 100 mgm. of utilizable organic matter per liter approximates the minimum concentration in which certain bacteria can grow. This is greatly in excess of the concentration of total organic matter commonly found in lakes; Lake Mendota water containing an average of only 12 mgm./1. (Birge and Juday, 1934); and, as will be shown below, much of this is highly refractory to bacterial decomposition. While many bacteria indigenous to natural waters can

TABLE III

Effect of the concentration of glucose upon the rate of respiration of "resting" bacteria in water which initially contained 7.28 mgm. of oxygen per liter.

Concentration of glucose	Oxygen consumed after			
	1 hour	2 hours	4 hours	8 hours
mgm./l.	*mgm./l.*	*mgm./l.*	*mgm./l.*	*mgm./l.*
0	0.06	0.10	0.14	0.23
2	0.12	0.19	0.38	0.53
5	0.16	0.26	0.52	0.91
10	0.17	0.34	0.71	1.18
100	0.29	0.63	1.43	1.69
1000	0.32	0.69	1.38	1.75

maintain themselves indefinitely when sub-cultured in lake water as well as in sea water which contains less than 10 mgm. of total organic matter per liter, this concentration seems to be in the neighborhood of their threshold for multiplication.

The effect of concentration of organic matter upon the rate of oxygen consumption was investigated by adding from 2 to 1000 mgm. of glucose per liter of synthetic lake water inoculated with enough washed bacterial cells (mixed microflora from Lake Mendota) to give around fifty million per ml. After different periods of incubation in oxygen bottles at 25° C. the amount of oxygen consumed was determined. The results are summarized in Table III. Although the "resting" cells were washed twice by centrifuging and re-suspending in synthetic lake water to free them of oxidizable materials, they consumed about 1.0 $\times 10^{-12}$ mgm. of oxygen per cell per hour without the addition of any

organic matter. However, the rate of respiration was increased by the addition of glucose until a concentration of 100 to 1000 mgm./l. was reached. Similar results were obtained with glycerol, asparagine and lactic acid. The rate of respiration was not influenced by the addition of 2 mgm./l. of either ammonium sulphate or potassium nitrate thereby proving that the lack of available nitrogen was not a limiting factor. Further experiments are planned to determine the effect of concentration of other organic compounds upon the respiration and other vital activities of bacteria.

TABLE IV

Relative rates of oxidation of 2.0 mgm./l. of organic compounds by cultures of lake bacteria as indicated by the amount of oxygen consumed after different periods of incubation at 25° C. The "oxygen demand" is the amount of oxygen required for the complete (100 per cent) oxidation of 2.0 mgm. of the compound.

Compound	Oxygen demand	Milligrams of oxygen consumed and per cent of each compound oxidized after					
		5 days		10 days		20 days	
	mgm.	*mgm.*	*per cent*	*mgm.*	*per cent*	*mgm.*	*per cent*
Succinic acid	0.88	0.42	47.8	0.63	71.6	0.83	94.4
Glycine	1.28	0.74	57.8	0.96	75.0	1.16	90.7
Asparagine	1.46	0.59	40.4	0.95	65.1	1.24	85.0
Lactic acid	2.12	1.29	60.9	1.76	83.0	2.10	99.1
Glucose	2.14	1.56	72.9	2.02	94.5	2.07	96.8
Starch	2.36	0.44	18.7	1.19	50.4	2.20	93.3
Cellulose	2.36	0.17	7.2	0.42	17.8	0.96	40.7
Glycerol	2.44	1.63	66.8	1.97	80.8	2.36	97.8
Propionic acid	3.04	0.72	23.7	1.38	45.4	2.24	73.7
Butyric acid	3.64	0.68	18.7	1.49	40.9	2.35	64.6
Lignin	3.70	0	0	0	0	0.23	6.2
Ethanol	4.16	2.06	49.6	3.12	75.0	4.01	96.4

The susceptibility to bacterial attack of different organic compounds which may occur in lacustrine materials was tested by adding 2.0 mgm./l. of the compounds to synthetic lake water (a mineral solution simulating lake water in composition but devoid of oxidizable substrates). The latter was inoculated with mixed microflora from Lake Mendota and distributed in 145 ml. glass-stoppered bottles. In the course of the experiment the bacterial population increased from an initial 26,000 per ml. to several million per ml. after 5 to 20 days incubation at 25° C. Dissolved oxygen was determined at the beginning of the experiment and after different periods of incubation. Some of the data are summarized in Table IV which shows the rapidity with which various com-

pounds are attacked by lake bacteria. Corrections have been made for the 0.07, 0.12 and 0.16 mgm./1. of oxygen which was consumed after 5, 10 and 20 days respectively in the inoculated controls to which no organic matter was added. The "oxygen demand" is the theoretical amount of oxygen required for the complete oxidation of 2.0 mgm. of the compound to carbon dioxide and water. The oxygen demand of the nitrogenous compounds would be somewhat higher if the ammonium resulting from their decomposition were oxidized to nitrite or nitrate.

From Table IV it will be observed that there is considerable difference in the amount of oxygen required for the complete oxidation of similar quantities of different compounds and that there is even a greater difference in the susceptibility of the compounds to bacterial decomposition. Part of the difference in the rate at which oxygen is consumed by bacteria in the presence of different compounds is attributable to differences in the number of bacteria in the mixed culture which are capable of attacking the given compound as well as to differences in the growth-promoting properties of the compounds. Moreover, the fact that the oxidation of some compounds requires four or five times as much oxygen as equal concentrations of other compounds might influence the results. An evaluation of these and other factors which are involved in the full interpretation of the experiment awaits further investigations but the experiment does indicate in a general way how small concentrations of certain organic compounds might influence oxygen consumption by bacteria in lake water. It seems especially noteworthy that 2.0 mgm./1. of some of the compounds are almost quantitively oxidized in 10 to 20 days and the more resistant compounds including cellulose and lignin are slowly oxidized by certain lake bacteria. Working with eleven samples of purified lignin differing either in source or method of preparation ZoBell and Stadler (1940*b*) found that 4.4 to 14.7 per cent of the lignin was oxidized by lake bacteria in 30 days at 28° C. Kinkel (1936) has reported on the decomposition of cellulose, chitin and pectin by aerobic bacteria found in Wisconsin lakes.

Lacustrine Organic Matter

Most of the organic matter which occurs in lake water is quite refractory to bacterial oxidation. This was demonstrated by noting the rate and amount of oxygen consumption in samples collected from various Wisconsin lakes at different times during the year. The water was collected in 5-gallon carboys, filtered through cotton gauze to remove gross particles, thoroughly shaken to insure uniformity in composition and after it was warmed to 25° C., the water was siphoned into 145 ml.

oxygen bottles. Duplicate bottles were analyzed for dissolved oxygen after different periods of incubation in the dark in a water bath at 25° C. Table V shows the oxygen-consuming capacity of Lake Mendota water collected near the surface at Station S 7 from October 11, 1938, to May 6, 1939. In February the samples were collected through twelve to twenty inches of ice.

Assuming the total organic matter content of Lake Mendota water to be 12 mgm./1., the average found by Birge and Juday (1926) over

TABLE V

Biochemical oxygen demand (B.O.D.) of Lake Mendota water from Station S 7 after different periods of incubation at 25° C. Upon equilibration with air at 25° C. the oxygen concentration of the water was around 8.5 mgm./l. at the beginning of each experiment.

Description of samples			Oxygen consumed after				Ratio 5:20 day B.O.D.
Date of collection	Oxygen content	Temperature of water	5 days	10 days	20 days	30 days	
	mgm./l.	*° C.*	*mgm./l.*	*mgm./l.*	*mgm./l.*	*mgm./l.*	*per cent*
10/11/38	8.96	16.4	2.06	—	3.84	5.14	53.6
10/25/38	9.08	15.1	2.30	3.82	4.51	5.58	50.9
11/ 2/38	9.37	12.8	2.17	3.73	4.17	—	52.1
11/ 9/38	10.62	8.5	1.54	2.22	3.32	3.96	46.4
11/21/38	11.54	6.6	1.60	2.40	3.41	4.09	46.8
11/30/38	11.93	5.2	0.97	2.07	2.42	3.15	40.2
12/ 8/38	12.45	3.4	0.86	1.65	2.00	2.23	43.0
12/16/38	13.86	1.6	0.96	—	2.14	—	44.4
1/ 4/39	13.08	0	1.36	2.42	3.02	4.21	45.1
1/11/39	14.34	0	1.50	2.31	3.31	4.18	45.4
1/23/39	13.72	0	1.29	—	3.22	3.86	40.2
2/ 6/39	12.90	0	0.91	1.37	2.30	2.60	39.4
2/20/39	12.74	0	0.84	1.21	1.92	—	43.8
3/ 7/39	12.31	0	1.24	1.95	2.99	3.99	41.5
3/23/39	14.18	0.3	3.11	4.66	6.20	7.13	50.2
4/10/39	11.80	7.4	3.56	5.22	7.25	—	49.1
5/ 6/39	10.37	11.6	3.92	5.38	7.46	—	52.5

a period of years, and since the complete oxidation of 1.0 mgm. of lacustrine organic matter requires an average of 1.2 mgm. of oxygen, it is estimated that only 21 to 30 per cent of the total organic matter is oxidized in 20 days, and 31 to 37 per cent in 30 days at 25° C. The prolonged incubation of a few samples showed that oxygen continued to be used at a decreasing rate, but after 94 days less than 50 per cent of the organic matter was oxidized. Using the evolution of carbon dioxide as the criterion of decomposition, Allgeier, Peterson and Juday (1934) found that from 18 to 42 per cent of the organic carbon in lake water

was oxidized in 31 days at 25° C. According to Waksman and Renn (1936), about 50 per cent of the organic matter in sea water is decomposed by bacteria under similar conditions; and of this decomposed organic matter, about 60 per cent is completely oxidized and about 40 per cent is converted into bacterial cell substance.

Upon the addition of 10 mgm./l. of glucose to the lake water all of the oxygen (about 8.5 mgm./l. at 25° C.) was rapidly depleted from the lake water thereby indicating that available nitrogen is not a factor which limits the oxidation of the organic matter in lake water. Moreover, neither the rate nor the amount of oxygen consumption was influenced by the addition of 2 mgm./l. of ammonium sulphate.

The respirable or oxidizable organic content of Lake Mendota water as indicated by its oxygen-consuming capacity was found to decrease

TABLE VI

Oxygen consumed by bacteria (B.O.D.) in samples of water from Northeastern Wisconsin lakes after different periods of incubation at 25° C.

Lake	Date of collection	Oxygen consumed after			Ratio of 5:20 day B.O.D.
		5 days	10 days	20 days	
		mgm./l.	*mgm./l.*	*mgm./l.*	*per cent*
Crystal Lake	1/12/39	0.52	1.34	1.86	28.7
Crystal Lake	2/25/39	0.44	0.95	1.57	28.1
Trout Lake	2/23/39	2.27	3.41	5.33	42.6
Silver Lake	3/29/39	0.83	1.55	2.07	40.2
Little Star Lake	3/29/39	2.12	3.31	5.04	42.1

from the time of the fall overturn in October until the ice started to melt late in March (see Table V). The melting of the ice was accompanied by much terrigenous contamination which might account in part for the sudden increase of oxidizable material at this time although other factors, including an increase of phytoplankton, are involved. According to Birge and Juday (1934) the organic matter content of Lake Mendota varies very little throughout the year, centrifuge plankton constituting less than 10 per cent of the total. However, the plankton forms appear to be decomposed much more rapidly and more completely than the resistant residual dissolved organic matter in lake water.

From 65 to 75 per cent of the organic matter in the net plankton concentrate added to synthetic lake water was found to be oxidized in 20 days at 25° C. Filtering Lake Mendota water collected during the spring months through No. 25 bolting silk which removes the larger plankton forms reduced its oxygen-consuming capacity 4 to 13 per cent.

The Foerst supercentrifuge (Juday, 1926) removed enough particulate organic matter to reduce the oxygen-consuming capacity of lake water 9 to 21 per cent.

The lower the concentration of oxidizable material in lake water the more refractory it is to bacterial attack. For example, from the last of November (11/30/38) to the first of March (3/7/39) when the 20-day B.O.D. of Lake Mendota water was lowest, the ratio of the 5-day B.O.D. to the 20-day B.O.D. was also lowest; or proportionately less oxygen was consumed in 5 days when the total oxidizable content was lowest (see Table V). Similar observations were made on water samples from other Wisconsin lakes as shown in Table VI. Less oxidizable organic matter was found and the ratio of the 5-day to the 20-day B.O.D. was lower in oligotrophic Crystal Lake than in eutrophic Trout, Little Star and Silver Lakes.

TABLE VII

Oxygen consumed per 100 mgm. (dry basis) of Lake Mendota mud dredged from Station 1 in January 1939 after different periods of incubation at 25° C.

Sample No.	Mgm. oxygen consumed after				Ratio of 5:20 day B.O.D.
	5 days	10 days	20 days	30 days	
1380	1.44	2.93	3.67	4.26	39.2
1390	1.25	3.03	4.34	4.63	28.8
1406	1.73	2.78	4.01	4.56	43.1
1409	1.09	1.97	3.58	3.96	30.2
Average	1.38	2.68	3.90	4.35	35.4

The amount of biochemically oxidizable material in Lake Mendota mud was estimated by diluting dredged samples a thousandfold or more with synthetic lake water. The diluted material was equilibrated with air to satisfy any chemical oxygen deficit (Miyadi, 1934), transferred to oxygen bottles with continued shaking to insure uniformity of composition and incubated in the water bath at 25° C. Duplicate bottles were analyzed for oxygen after different periods of incubation. Table VII summarizes the results. The relative slowness with which oxygen is consumed (5:20-day B.O.D. equals 35.4 per cent) shows that the material in the mud is more resistant to bacterial attack than that in Lake Mendota water. Similarly Waksman and Hotchkiss (1938) found that the organic matter in marine bottom deposits is oxidized less readily by bacteria than that in sea water.

According to Black (1929) mud from Station 1 in Lake Mendota contains an average of 13 per cent organic matter (dry basis). As-

suming that 1.2 mgm. of oxygen is required for the complete oxidation of 1.0 mgm. of the organic matter, it is calculated that 24 per cent of the organic matter in the lake deposits is oxidized aerobically in 20 days and around 29 per cent is oxidized in 30 days at 25° C. Decomposition continues slowly thereafter at a constantly decreasing rate. The organic matter in the mud is decomposed much more readily in the presence of oxygen than anaerobically because Allgeier et al. (1932) found that only 1 per cent of the total organic carbon was destroyed in 7 months under anaerobic conditions. Steiner and Meloche (1935) have shown that from 30 to 48 per cent of the organic matter in lake deposits consists of ligneous materials which are very resistant.

Little relationship was noted between the oxidizability of the lacustrine materials by permanganate (Wereščagin et al., 1931) and its oxidizability as indicated by oxygen consumption by bacteria. The latter is believed to be much more representative of the capacity of the organic matter to utilize oxygen *in situ*.

Discussion

If the heterotrophic bacteria in Lake Mendota consume oxygen at the rate of 9 to 20×10^{-12} mgm. per cell per hour (values found in the laboratory at 8° and 18° C. respectively), a hundred thousand bacteria per ml. would consume 4 to 9 mgm. of oxygen per liter of water during the six summer months when the temperature of the water ranges from 8° to 18° C. At this rate the activities of heterotrophic bacteria could account for the depletion of the oxygen from stagnant waters particularly in the lake bottom where bacterial populations exceeding a million per ml. have been demonstrated (Henrici and McCoy, 1938). While these estimates based upon laboratory observations are highly speculative, they substantiate the conclusions of field workers that bacteria probably play a very important rôle in the utilization of oxygen in lakes. When more complete data become available it should be possible to evaluate with greater precision the rôle of bacteria. Combining field and laboratory observations Liagina and Kusnetzow (1937) have calculated that "the decrease of the oxygen content of the waters of Lake Glubokoje can be covered with excess by the respiration of the water bacteria."

Although little is known concerning the abundance and activity of chemosynthetic autotrophic bacteria in lakes, those which oxidize ammonium, nitrite, hydrogen sulphide and methane may utilize appreciable quantities of oxygen. The possible significance of such autotrophs is apparent from the fact that the oxidation of 1.0 mgm. of ammonium to nitrate requires 5.15 mgm. of oxygen, the oxidation of 1.0 mgm. of

hydrogen sulphide to sulphate requires 4.23 mgm. of oxygen and the oxidation of 1.0 mgm. of methane to carbon dioxide and water requires 4.0 mgm. of oxygen. Hydrographic data (Welch, 1935) indicate the presence of from a trace to a few milligrams per liter of ammonium, hydrogen sulphide and methane in lake water from various places and there is evidence that these substances are oxidized. Kusnetzow (1934) believes that methane-oxidizing bacteria consume more oxygen in certain lakes than all other bacteria and animals combined. According to Ravich-Sherbo (1930) there is an extensive layer of sulphur bacteria in the Black Sea where they oxidize the hydrogen sulphide from the hypolimnion at the expense of the oxygen from the epilimnion. A similar localization of sulphur bacteria in the marginal zone of Lake Ritom has been reported by Düggeli (1924).

Summary

The rate of respiration of lake bacteria increases with temperature, the Q_{10} from 8° to 25° C. being 2.1. Mixed microflora from Lake Mendota were found to consume from 21 to 43×10^{-12} mgm. of oxygen per cell per hour at 25° C. Prolonged exposure at 37° C. is injurious to some of the bacteria.

The rate of respiration is independent of the oxygen concentration of the water within the examined range of 0.31 to 26.48 mgm./l. As the oxygen tension is reduced below 0.3 mgm./l. the rate of bacterial respiration decreases rapidly.

Both the character and the concentration of organic matter influence the rate of oxygen consumption by lake bacteria. The rate of respiration of " resting " cells increases as the concentration of glucose, asparagine and lactic acid is increased up to 100 to 1000 mgm./l.

About one-third of the organic matter in Lake Mendota water is readily oxidizable, the remainder being quite resistant to bacterial attack. The organic content of bottom deposits is less oxidizable than that of water, and the remains of plankton organisms are more readily oxidized by bacteria than the dissolved organic matter occurring in lake water.

Acknowledgment

The author is indebted to Miss Janice Stadler and Dr. F. Cho for technical assistance and to Dr. Elizabeth McCoy, Dr. E. B. Fred, Dr. E. A. Birge and Dr. Chancey Juday for their encouragement and constructive criticisms.

REFERENCES

Allgeier, R. J., W. H. Peterson, and C. Juday, 1934. Availability of carbon in certain aquatic materials under aerobic conditions of fermentation. *Int. Rev. ges. Hydrobiol.*, **30**: 371–378.

Allgeier, R. J., W. H. Peterson, C. Juday, and E. A. Birge, 1932. The anaerobic fermentation of lake deposits. *Int. Rev. ges. Hydrobiol.*, **26**: 444–461.

Amberson, W. R., 1928. The influence of oxygen tension upon the respiration of unicellular organisms. *Biol. Bull.*, **55**: 79–91.

Baier, C. R., 1935. Studien zur Hydrobakteriologie stehender Binnengewässer. *Arch. f. Hydrobiol.*, **29**: 183–264.

Birge, E. A., and C. Juday, 1911. The inland lakes of Wisconsin. I. The dissolved gases of the water and their biological significance. *Bull. Wis. Geol. and Nat. Hist. Survey*, **22**: 1–259.

Birge, E. A., and C. Juday, 1926. Organic content of lake water. *Bull. U. S. Bur. Fish.*, **42**: 185–205.

Birge, E. A., and C. Juday, 1934. Particulate and dissolved organic matter in inland lakes. *Ecol. Monographs*, **4**: 440–474.

Black, C. S., 1929. Chemical analyses of lake deposits. *Trans. Wis. Acad. Sci.*, **24**: 127–133.

Buchanan, R. E., and E. I. Fulmer, 1930. Physiology and Biochemistry of Bacteria. Williams and Wilkins Co., Baltimore, vol. 3, p. 154.

Clifton, C. E., and W. A. Logan, 1939. On the relation between assimilation and respiration in suspensions and in cultures of *Escherichia coli*. *Jour. Bact.*, **37**: 523–540.

Domogalla, B. P., E. B. Fred, and W. H. Peterson, 1926. Seasonal variations in the ammonia and nitrate content of lake waters. *Jour. Am. Water Works Assoc.*, **15**: 369–385.

Düggeli, M., 1924. Bakteriologische Untersuchungen am Ritom-See. *Rev. d'Hydrolog.*, **2**: 65–205.

Edwards, O. F., and L. F. Rettger, 1937. The relation of certain respiratory enzymes to the maximum growth temperatures of bacteria. *Jour. Bact.*, **34**: 489–515.

Friedlein, F., 1928. Der quantitative verwendungstoffwechsel des Paratyphus B–Bazillus, des Bacterium coli und des Bacillus pyocyaneus. *Biochem. Zeitschr.*, **194**: 273–291.

Grote, A., 1934. Der Sauerstoffhaushalt der Seen. *Die Binnengewässer*, **14**: 1–217.

Harvey, E. N., 1928. The oxygen consumption of luminous bacteria. *Jour. Gen. Physiol.*, **11**: 469–475.

Henrici, A. T., and Elizabeth McCoy, 1938. The distribution of heterotrophic bacteria in the bottom deposits of some lakes. *Trans. Wis. Acad. Sci.*, **31**: 323–361.

Heukelekian, H., 1936. Oxygen tension and bacterial numbers. *Sewage Works Jour.*, **8**: 415–421.

Juday, C., 1926. A third report on limnological apparatus. *Trans. Wisconsin Acad. Sci.*, **22**: 299–314.

Juday, C., E. B. Fred, and F. C. Wilson, 1924. The hydrogen ion concentration of certain Wisconsin lake waters. *Trans. Am. Micros. Soc.*, **43**: 177–190.

Kempner, W., 1937. Effect of oxygen tension on cellular metabolism. *Jour. Cell. and Comp. Physiol.*, **10**: 339–363.

Kinkel, Dorothy, 1936. A study of chitin-, pectin- and cellulose-destroying bacteria from lake mud. Dissertation, University of Wisconsin, 35 pp.

Kusnetzow, S. I., 1934. Microbiological investigations in the study of the oxygen regime of lakes. *Microbiol.*, **3**: 486–505 (Russian).

KUSNETZOW, S. I., AND G. S. KARSINKIN, 1931. Direct method for the quantitative study of bacteria in water and some considerations on the causes which produce a zone of oxygen-minimum in Lake Glubokoje. *Centralbl. f. Bakt.*, II Abt., **83**: 169–174.

LIAGINA, N. M., AND S. I. KUSNETZOW, 1937. The determination of the intensity of respiration of some species of water bacteria at various temperatures under laboratory conditions. *Microbiol.*, **6**: 21–27 (Russian with English summary).

MIYADI, D., 1934. Oxygen absorption of the lake deposit. *Proc. Imperial Acad.*, **10**: 236–239.

POMEROY, R., 1938. Influence of oxygen concentration on biochemical oxygen demand. *Sewage Works Jour.*, **10**: 465–472.

PÜTTER, A., 1924. Die Atmung der Planktonbakterien. *Pflügers Arch. f. Ges. Physiol.*, **204**: 94–126.

RAVICH-SHERBO, J., 1930. On the question of the bacterial thin layer in the Black Sea according to the hypothesis of Prof. Egounoff. *Travaux de la Station Biologique de Sebastopol.*, **2**: 127–141.

SCHLAYER, C., 1936. The influence of oxygen tension on the respiration of Pneumococci (Type I). *Jour. Bact.*, **31**: 181–189.

SEIWELL, H. R., AND GLADYS SEIWELL, 1938. The sinking of decomposing plankton in sea water and its relationship to oxygen consumption and phosphorus liberation. *Proc. Amer. Phil. Soc.*, **78**: 465–481.

STEINER, J. F., AND V. W. MELOCHE, 1935. A study of ligneous substances in lacustrine materials. *Trans. Wis. Acad. Sci.*, **29**: 389–402.

THIENEMANN, A., 1928. Der Saurstoff im eutrophen und oligotrophen See. *Die Binnengewässer*, **4**: 1–175.

WAKSMAN, S. A., AND CORNELIA L. CAREY, 1935. Decomposition of organic matter in sea water by bacteria. I. Bacterial multiplication in stored sea water. *Jour. Bact.*, **29**: 531–543.

WAKSMAN, S. A., AND MARGARET HOTCHKISS, 1938. On the oxidation of organic matter in marine sediments by bacteria. *Jour. Mar. Res.*, **1**: 101–118.

WAKSMAN, S. A., AND C. E. RENN, 1936. Decomposition of organic matter in sea water by bacteria. III. Factors influencing the rate of decomposition. *Biol. Bull.*, **70**: 472–483.

WELCH, P. S., 1935. Limnology. McGraw-Hill, New York, 471 pp.

WEREŠČAGIN, G. J., N. J. ANIČKOVA, AND T. B. FORSCH, 1931. Methoden der hydrochemischen Analyse in der limnologischen Praxis. *Arch. f. Hydrobiol.*, **23**: 167–230.

ZOBELL, C. E., AND D. Q. ANDERSON, 1936. Observations on the multiplication of bacteria in different volumes of stored sea water and the influence of oxygen tension and solid surfaces. *Biol. Bull.*, **71**: 324–342.

ZOBELL, C. E., AND JEAN E. CONN, 1940. Studies on the thermal sensitivity of marine bacteria. *Jour. Bact.*, **40**: (In press).

ZOBELL, C. E., AND JANICE STADLER, 1940*a*. The effect of oxygen tension on the oxygen uptake of lake bacteria. *Jour. Bact.*, **39**: 307–322.

ZOBELL, C. E., AND JANICE STADLER, 1940*b*. The oxidation of lignin by lake bacteria. *Arch. f. Hydrobiol.* (In press).

Contribution No. 97

The Naturalist as a Social Phenomenon

DR. FRANCIS B. SUMNER

Reprinted from THE AMERICAN NATURALIST, Vol. LXXIV,
pages 398–408, September–October, 1940.

THE NATURALIST AS A SOCIAL PHENOMENON[1,2]

DR. FRANCIS B. SUMNER
SCRIPPS INSTITUTION OF OCEANOGRAPHY

I PRESUME that I have been included among the speakers in to-day's symposium merely for the reason that I am an old friend and admirer of Dr. Ritter's and not because I am really expected to contribute any ideas of importance on the "biological basis of social problems." Indeed, the title which I first suggested for this discourse was quite a different one from that which appears on our program. It was: "Is There Any Present-Day Need for a Society of Naturalists?" But Dr. Taylor readily convinced me that such a title would not harmonize very well with the general title of this symposium.

Nevertheless, the rhetorical question which I have just set before you springs from an obsession of mine of long standing, and this is such an insistent one that I shall devote a considerable part of my time to the attempt to answer it.

Let us consider first, however, some of the implications of the title actually adopted: "The Naturalist as a Social Phenomenon." The thought at once arises: How could the naturalist, or any other scientist, exist except as a social phenomenon? Leaving out of account the considerable cultural background which must develop before science is possible, it seems evident that the motivation of the individual scientist is necessarily largely social.

We as a group are often credited by idealistic writers, outside of our own profession, with a "disinterested love" of some abstraction called "Truth," or "Science," or what not. Of course we have too much sense to believe that sort of stuff ourselves. But we are, I think, prone to believe that we are actuated primarily, if not exclu-

[1] Read at a symposium on "The Biological Basis of Social Problems" held in honor of Professor William E. Ritter at the meeting of the Western Society of Naturalists, Monterey, Calif., December 20, 1939.

[2] Contribution from the Scripps Institution of Oceanography, New Series, No. 97.

sively, by our intellectual interest in what we are doing. How far is that really true?

I have confronted myself, and various of my colleagues, with some more or less embarrassing questions, which are not, I presume, altogether original with me. Would you keep on making these interesting observations if publication or any other outlet for your discoveries were denied you? I think that I hear an almost unanimous negative reply to the question. Frankly, it is the reply which I myself should give. I admit that the conditions suggested would be rather rough on you. So we'll let you publish your discoveries in full, but with the proviso that they shall always remain anonymous. No one but yourself would ever know the secret of their authorship. I have a strong conviction that you would still hesitate, and that if you really decided to go ahead, it would be with vastly diminished zest. At least, I may so speak for myself. Nor is this necessarily a confession of vanity or selfishness. It is merely another bit of evidence that even *Homo scientificus* is a gregarious species. Our satisfactions are derived largely from the approbation and sympathetic understanding of our colleagues, from the interchange of ideas and—in very varying degree, it is true—from the belief that this hard-won increase in knowledge is, on the whole, a good thing for mankind. This last assumption is, of course, the only justification for the public support of scientific work, and I believe that the assumption is fully warranted. But the degree to which the individual scientist is motivated by such considerations is certainly highly variable. It is only too evident that in extensive areas of the world at present, important fields of science are being exploited for purposes quite other than human welfare. However, we naturalists may take satisfaction in the knowledge that none of the discoveries which we make in our field lends itself very well to the butchery of our colleagues who speak some other language.

What, then, is the peculiar field of the naturalist? My

past remarks, for the most part, would apply equally well to scientists of any sort. I shall not bore you with any attempt to define this term. Several quite different meanings are attached to the word, as will be found by glancing into a dictionary. What I mean here by a naturalist will develop in the course of the ensuing remarks.

I fear that the word is one which too often arouses feelings of antipathy or contempt in the mind of the modern biologist. It is difficult to escape the popular caricature: a wizened, bespectacled individual, who spends his time sorting and naming pickled specimens or endless rows of insects—an eccentric whose chief outdoor diversion consists in sweeping the air with a butterfly-net or gathering snakes and spiders in his wife's cooking utensils. At best, we are apt to think of a naturalist as an unfortunate who has not been able to keep up with the procession of those who are making the real advances in biology. Indeed, we are wont to prefix the words "old fashioned" when we apply this term to anyone.

What, then, is a naturalist? To say that he is a person who concerns himself with natural history would not, I am afraid, be very helpful in clearing our friend's reputation. For the expression "natural history" even more suggests something altogether primitive and out-of-date —a pursuit suited only to children and amateurs. Indeed, we learn from "Webster's Dictionary" that this term is "now commonly restricted to a study of these subjects [zoology and botany] in a more or less superficial way, at least without making use of modern anatomical and analytical methods." And a glance at the endless popular volumes carrying the title of "natural history" would seem to bear out this statement.

Are we, however, forced to accept such a depreciation of a term which has had such long and honorable associations? Listen to the words of one of our greatest naturalists, William Morton Wheeler:

> History shows us that throughout the centuries, from Aristotle and Pliny to the present day, natural history constitutes the perennial root-stock or

stolon of biological science and that it retains this character because it satisfies some of our most fundamental and vital interests in organisms as living individuals more or less like ourselves. From time to time the stolon has produced special disciplines which have grown into great, flourishing complexes. . . . The stolonic relationship of natural history, or ecology, to the other biological disciplines is of great theoretical and practical significance. Nearly all the important biological problems, especially of a physiological or morphological character, have arisen in the course of simple investigation in natural history and many of the more difficult of them have been turned over to the special disciplines for solution. On the other hand, the ecologist is continually drawing on the methods and resources of physiology, morphology, taxonomy, distribution, etc., in solving his own particular problems of adaptation and behavior.

It is evident that Wheeler's use of the word "ecology," in this connection, is considerably broader than that given it by the societies and journals which bear that name.

Wheeler's metaphor of the stolon seems to me admirable, though it is defective in one respect. For the individual plants or animals which are budded off from a stolon are capable of detaching themselves from the parent stock and becoming independent organisms. Our specialized branches of biology, on the contrary, can not live independently of the parent stock and in so far as they attempt to do so, they languish. (All this Wheeler himself would, of course, have insisted upon.)

We may state this last idea differently by stressing the importance of maintaining the natural history point of view, whatever specialty one may happen to be pursuing. Regarded from this angle, we might consider anyone to be a naturalist who consistently maintained the natural history point of view. This is the point of view which looks beyond the immediate object of one's pursuit and does not lose sight of its relations to a larger whole. It stresses synthesis as a necessary complement to analysis, integration as a necessary complement to differentiation.

The naturalist, as thus conceived, never forgets that he is dealing with organisms dwelling in environments, even though he may be concerned for the moment with cells, chromosomes, genes, sols, gels, ions, unsaturated valencies or what not. He recognizes the autonomy of biology as a science, and does not lose interest in those activities

of organisms which he can not subject to physical or chemical analysis. In general, I think that he will subscribe to the dictum of Dr. Ritter that "the organism in its totality is as essential to an explanation of its elements as its elements are to an explanation of the organism."

I am tempted to add that in the field of taxonomy the naturalist, as thus described, is more likely to be a "lumper" than a "splitter," though I confess that this is merely a wild guess, based upon my notions of the fitness of things. For the "lumper" is a person who recognizes the importance of stressing resemblances as well as differences, of synthesis as well as analysis.

Do I seem to be wandering too far from the subject-matter of this symposium? I think that I am hewing to the line. What can be of more importance socially than the integration of our knowledge—the assimilation of each new discovery to the past acquisitions of our race? On the contrary we may well query whether extreme specialization may not at times become an anti-social process. When it loses its sense of perspective and adopts an esoteric vocabulary and ideology, does it not actually become an eddy moving in the wrong direction?

Even these references to taxonomy really have a very distinct social slant, as I was long ago moved to point out. For the unchecked splitting of genera results not only in creating confusion in the terminology which we are all forced to use, but it destroys what we may call the "verbal clues to the nearer kinships between species." This situation handicaps a group much wider than that of the professional biologists.

It may be pertinent at this point to recall the question which I put before you at the outset: "Is there any present-day need for a society of naturalists?" I do not have in mind merely a question of name. I have in mind the subjects to be discussed by such an organization, and more yet the manner of their treatment. We have our special societies, which now represent almost every minutest subdivision of the life sciences. It is not my object to deplore

the specialization here implied. This seems to be the price which we must pay for advance in science.

Should there not remain, however, a few organizations which specialize, so to speak, in the more general aspects of biology; which maintain consistently the naturalist's point of view? A society is at least conceivable having as its primary object the presentation of programs calculated to be intelligible and interesting to all members of a diversified audience such as the present one. By this I do not have in mind providing popular programs for the laity. That is quite another problem. I am thinking of ourselves. I have in mind the need among workers in diverse branches of biology, for cultivating and extending such common ground as still remains to us in spite of our increasing specialization. It would not be possible or even desirable, to limit the programs of such a society to discussions in the field of general biology. Reports of individual researches might be welcomed as usual, but with certain very important restrictions. The society should insist that every paper admitted to its program must rise above the merely descriptive level, and that its author must make it clear why we should be interested in what he is telling us.

Or is this a counsel of perfection? Perhaps it is. At least, I have often been told so. And yet I am so convinced that the contrary is true that I have bored some of my colleagues for years with my protestations. Not that these persons do not admit the deplorable condition of so many of our scientific programs, but they adopt a defeatist attitude and argue that the situation is incurable.

One is inevitably met with the challenge: How many of our biologists, particularly our younger ones, are capable of interesting a group as diversified as this? I fear it is true that sufficient attention has never been devoted to training our graduate students to be interesting. Since most of them are merely going to be teachers, perhaps this has not been regarded as important. However, I think it might have a salutary effect if we admitted to our an-

nual programs only those who have made some progress in the art of being interesting. Let the impression get around that it is an honor to present a paper at one of our meetings, and that only the more competent men can make the grade. The practice in the past has too often been to accept with thanks anything that is offered. Is not the alternative plan worth more serious consideration? It might shorten our programs, perhaps, but would that be an unmixed evil?

This matter of being interesting includes, of course, something far more than mere literary or rhetorical skill. It includes the ability to see the broader implications of one's discoveries and to present them intelligibly to persons who are not fellow-travelers in one's own particular compartment. If these broader implications are not discernible, the paper does not belong on the program of a society of naturalists at all. There are more highly specialized organizations before which such communications may be presented.

I must add that these later remarks of mine have a much broader application than merely to our hypothetical society of naturalists. The criteria of interest and intelligibility should be applied even to our more narrowly specialized programs. That these criteria are not sufficiently adhered to has resulted in a situation so often expressed in the declaration: "I don't attend the meetings to listen to papers; I go to visit with my friends." Such an attitude is unduly pessimistic, I think, but we must admit that it has considerable justification.

Regarding the kind of material appropriate for the programs of a society of naturalists, I fear that my remarks thus far have been rather indefinite. Suppose that we get down to cases. It is naturally much easier to pick out examples of things that do not belong on such programs than it is to offer helpful suggestions along constructive lines. This because the pages of our technical journals are filled almost exclusively with material of the former class. Here are a half dozen titles which I jotted

down a few days ago from the contents of recent issues of an equal number of leading American biological journals. They are, I think, quite representative ones. As contributions to the literature these papers are all, perhaps, impeccable. But my hypothetical censor would exclude every one of them from the program of a society of naturalists. It is even possible that an intelligent and sufficiently hard-boiled censor would rule that some of these were unsuited for presentation to any audience comprised of more than six persons. Here are the samples:

An analysis of the chromosomes of the two subspecies *Drosophila virilis virilis* and *Drosophila virilis americana.*

A new race of sharp-shinned hawk from Mexico.

Activity-preventing and egg-sea-water neutralizing substances from spermatozoa of *Echinometra subangularis.*

The functional significance of the capillary bed in the brain of the opossum.

Effect of the introduction of the nitro group into the phenol molecule on toxicity to goldfish.

Experimental study of the function of the corpora allata in the grasshopper *Melanoplus differentialis.*

This is no carefully selected list. It represents a fair sampling of the titles which make up the tables of contents of these various journals. They reflect the prevailing modes in biological research. They all probably represent profitable lines of research.

To pick out an equal number of papers to illustrate the kind which I believe to be suitable for presentation before a society of naturalists is much more difficult. Practically nothing of promise in this direction is to be found in any of the six journals from which the preceding list was taken. One thinks at once of the AMERICAN NATURALIST in this connection. But for years the contents of this journal, with the exception of the symposia which it publishes, have been for the most part highly specialized. Many of the contributions might equally well have appeared in one of the journals of genetics. It is interesting to compare the successive volumes of this important periodical from its inception in 1868 to the present day. We have a pageant of the history of biology in America. It is a long way from Morse and Packard and Hyatt and

Cope to Morgan and Jennings and Child and Parker. Nor can we deny that this trend, on the whole, represents progress.

The sort of material that we are looking for now is best exemplified in the subject-matter of some of the symposia, published in the AMERICAN NATURALIST. (I may add, in the subject-matter of some of the symposia of our present meeting.) Such topics as "Adaptation," "Temperature and Life," "The Species Problem," "The Biology of Sex," "The Cell Theory" and "Contributions of the Higher Animals to an Understanding of Human Biology" surely belong to the realm of natural history in the sense which Wheeler had in mind.

I think none of us, however, would wish to restrict our programs to symposia. Single contributions, invited or volunteered, which meet the requirements of relevancy would probably continue to furnish the backbone of the program.

Since I have said so much about relevancy, it seems a fair request that I should cite the titles of some papers which I should expect our naturalist-censor to admit to his program, though it is obvious that the title alone would not guarantee the acceptability of a paper. With some hesitation I offer another list of six titles which I jotted down after a much more prolonged search than that required for the first list. It would have been a much simpler matter to invent a series of such titles, but it is my wish to restrict myself here to actual ones:

Biological effects of population density in lower organisms.

Genetics of quintuplets.

The toleration of solar heat in desert reptiles.

Homing instinct in salmon.

Facts and theories of bird flight.

Survival value of acridian protective coloration.

It happens that this list is predominantly ecological in its complexion. But this was because the majority of available titles which I encountered were ecological ones. I do not see, however, why discussions based upon the

data of almost any one of the recognized sub-divisions of biology should not be relevant to a naturalists' program if properly handled. But the physiologist should not address himself primarily to the physiologist, nor the geneticist to the geneticist, nor the embryologist to the embryologist. Each should phrase his discussion as little as possible in the peculiar vocabulary of his specialty, and should make a determined endeavor to keep in view the broader significance of the data which he reports.

In fact, I seriously question whether such an organization as we have been discussing should be conducted primarily as a publicity channel through which its members may report their very latest series of experiments or observations. If it is really our object to be mutually informative, would not this object be far better achieved if we presented carefully digested reviews covering the general fields in which our particular research problems lie? Could not the detailed reports of progress usually be better left to our published accounts in the journals? Must we really lose caste by serving for the moment as teachers of one another?

Is all this sort of thing possible, or is it just another "Ham-and-Eggs" proposal? While I am not offering any precise mechanism by which these beneficent results could be achieved, I believe that they could be achieved if we really took the matter seriously. It would, perhaps, require the same degree of ingenuity that we all so cheerfully devote to our experimental problems in the laboratory—also, a considerable amount of hard work.

The essence of the plan, of course, is the selection of material for the programs. I confess that the picture of a hard-boiled censor is not a pretty one. I am afraid that he would not last very long in an American scientific society. But some benign selective agency is necessary for the purpose of soliciting appropriate material and rejecting what is inappropriate. Why should it be any more ruthless for a qualified program committee to reject a paper from its program than for the editors of a journal

to reject an unsuitable manuscript offered them for publication? Why indeed, could not this committee assume some of the friendly advisory functions which our editors perform in relation to the contributions offered them? There is often a third alternative besides outright acceptance or rejection.

I am quite aware that the line between topics which are "relevant" and those which are "irrelevant" to a given program must, at times, be very difficult to draw. Particularly is it difficult to judge by the title of a paper. I have in mind one rather recent case in which a man offered a contribution in the field of ichthyology, which turned out, when delivered, to be little more than a fervid eulogy of the government of Soviet Russia. Our censor had momentarily relaxed his vigilance. It seems reasonable to require that a completed manuscript, or at least a detailed summary of a paper, should be submitted in advance, as indeed is often done now.

Finally, it must be admitted that less depends upon the topic chosen than upon the way it is treated, in other words, upon the mental outlook of the speaker. One of the most harassing program numbers that ever drove me from a lecture-room was delivered by a contributor to an important symposium, a man apparently chosen because he was an "outstanding authority" in his particular specialty, but with no regard for his sense of proportion or ability to rise above the level of particulars. Here again, our censor had gone to sleep at the wheel.

On the other hand, a speaker who views his subject *sub specie aeternitatis* can make almost any bit of information illuminating. Such are our great lecturers in biology, men of the caliber of Edmund B. Wilson and G. H. Parker.

I think that you will agree with me that a naturalist who can bring to pass the beneficent things that I have been talking about will be not only a social phenomenon but a most valuable social asset. I do not wish to imply that we have not already made considerable progress in that direction, but I think that we still have a long distance to travel.

Contribution No. 98

REPRINTED FROM
BIOLOGICAL REVIEWS, VOL. 15, 1940, p. 351
[*All rights reserved*]
PRINTED IN GREAT BRITAIN

QUANTITATIVE CHANGES IN PIGMENTATION, RESULTING FROM VISUAL STIMULI IN FISHES AND AMPHIBIA[1]

By FRANCIS B. SUMNER

(Scripps Institution of Oceanography of the University of California, La Jolla, California)

(*Received* 15 *January* 1940)

CONTENTS

		PAGE
I.	Introduction	351
II.	Effects of background upon the formation or loss of pigment	353
III.	Intensity of illumination	361
IV.	Blinding	362
V.	Direct illumination with coloured light	362
VI.	Illumination from below	363
VII.	Some implications of the response to background	364
VIII.	The relation between "physiological" and "morphological" colour changes	366
IX.	Nervous and hormonal control of chromatophores	368
X.	Summary	370
XI.	References	372

I. INTRODUCTION

It is hardly necessary at this time to state that the familiar rather rapid colour changes which are undergone by various cold-blooded animals are not due to changes in the amount of pigment present. Even the most striking of such changes result from shifts in the position of pigment particles which do not vary in amount from moment to moment. It is pretty generally agreed, furthermore, that this rearrangement of pigment matter takes place within the limits of cells which maintain nearly constant outlines. Amoeboid movements of the chromatophores are believed to play a minor role, if any, at least in adult animals.

It has for some time been recognized, however, that there are other, more enduring changes of colour or shade which are due to actual changes (increase or decrease) in the amount of pigment in the tissues of the organism. These have been designated as "morphological" colour changes, in contradistinction to the former or "physiological" type of changes. It is clear that these terms are not very appropriate, inasmuch as both of these processes are equally *physiological*. It seems hardly practicable to dispense with them altogether, however, owing to the lack of a suitable pair of antonyms. I have, nevertheless, wherever possible, substituted "transitory" for "physiological" and "quantitative" for "morphological". It is interesting that a vast majority of the published papers in the field of colour change

[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 98. Assistance is acknowledged from W.P.A. Project 665–03–3–141.

have dealt with these immediate transitory or "physiological" responses of the chromatophores. Indeed, Fuchs, in his monumental review of colour change in animals (1914), appears to question the existence of quantitative ("morphological") colour change in response to optical stimuli, and von Buddenbrock, as late as 1928, was aware of no convincing evidence for fishes.

The present review will be concerned with quantitative changes only, except in so far as transitory changes are believed to be causally related to these. Under "quantitative" changes are here included any changes in the amount of pigment whether or not these have been submitted to actual measurement. This review will further be restricted to such pigmental changes as result from visual stimuli, or the withdrawal of these. The effects upon pigmentation of various other physical and chemical stimuli and of food cannot be considered here. Nor can the numerous and important studies of invertebrate animals be included.

For the purposes of the present discussion, the visual (optic) environment must be divided into (1) incident light and (2) the background. Such a division may seem to be an altogether artificial one, since most organisms can hardly be supposed to recognize the distinction between the source of light and the light which is reflected from surrounding objects and the substratum. However, the difference is of vital importance. Poikilochromic[1] animals respond in a high degree to differences in the shade or colour of the background, much less to differences in the intensity of the incident light. This is not at all mysterious when we recognize that the distinction here drawn is altogether a topographic one. The "background" comprises that part of the visual field which lies below a certain level, while "incident light" comprises that part which lies above that level. The contrasted effects of these two portions of the visual field depend, as will be pointed out below, upon functional differences in the upper and lower halves of the retina.

So far as shade (paleness or darkness) is concerned, the response of an animal to its background is a response to the latter's albedo. By albedo is here meant the proportion of incident light which is reflected or dispersed from a given surface. It is what makes the difference, for example, between white and a neutral grey. Thus the pigmentary response, whether "physiological" or "morphological", is largely independent of the absolute degree of illumination. It is not, however, wholly independent of this.

In the two preceding paragraphs it was assumed that we were dealing with white light. Illumination by limited portions of the spectrum have, however, been employed by a number of investigators, and have been found to exert specific effects upon the chromatophores of some organisms, and even upon pigment formation. In these cases, the quality of the incident light has been effective, quite independently of the background.

Numerous other experiments have been performed which deal with special modifications of the visual field: inverted illumination, total darkness, blinding, etc.

Investigations of chromatophore responses have had to do chiefly with the

[1] This term, which I have already employed (1935), seems a legitimate analogue of such terms as poikilothermic.

black cells (melanophores); to a far less extent with the white cells (guanophores) or the coloured cells (lipophores). This is because the melanophores are far more conspicuous than the other types of chromatophores, and are far more resistant to fixing and clearing reagents. Some important observations have, however, been made upon both guanophores (iridocytes) and lipophores. Quantitative determinations, in the case of melanophores, have consisted in either counting the actual number of these cells in a selected area of the skin, or in assaying the amount of melanin in the body as a whole. Both of these procedures have likewise been employed in the case of lipophores (at least of xanthopores). So far as I know, no precise determinations have been reported for guanophores.

Some of the phenomena here considered raise questions of great interest in the field of theoretical biology. Considerable portions of this review must accordingly be devoted to the discussion of such questions.

II. EFFECTS OF BACKGROUND UPON THE FORMATION OR LOSS OF PIGMENT

(1) *Melanin*

So far as I know, Flemming (1882, cited in 1897) was the first to point out that the shade of the background might be influential in modifying the quantity of pigment in an animal. The experiment to which Flemming refers was concerned with the effect of a white background upon the pigment of salamander larvae. He does not seem to be altogether certain, however, as to the nature of the effective stimulus.

Šecérov (1909) exposed the loach, *Nemacheilus barbatulus*, to various backgrounds, coloured and uncoloured, apparently with pronounced results upon the quantity of visible pigment. Some of this writer's claims are incredible, however (see below), a circumstance which must be borne in mind in evaluating his work. Šecérov seems to have been the first to employ the terms "physiological" and "morphological" colour change, and was perhaps the first to recognize the distinction between the classes of phenomena thus designated.

Franz (1910), experimenting upon young plaice, noted that these acquired chromatophores when they left off swimming and took up life upon the bottom. He gave reasons for believing that this was due to stimuli from the bottom, and not merely to an advance in the stage of development. Franz's interpretation of these facts is, however, quite untenable.

Babák (1910, 1912, 1913) made the first substantial contribution to our knowledge of the quantitative effects of visual stimuli upon pigmentation in vertebrates, and the mechanism by which these effects are produced. This investigator experimented with *Amblystoma* larvae, of which normal individuals were reared upon white and black backgrounds, blinded ones in the light and in darkness. Some of these were kept nearly six months, the number of chromatophores in several regions of the body being counted at intervals. He reports that at the end of this period an individual on black had nearly twice as many chromatophores as one on white. The increase in number per week was forty for the "black" animal, eleven for the "white" one. In this case, therefore, there was no absolute decrease in the

"white" specimen, but only a marked retardation in the rate of increase. Elsewhere he reports an actual reduction in the number of chromatophores previously present. Babák also points out that aside from these changes in number there may be a marked increase or decrease in the melanin content of the individual cells.

"There is thus no doubt", asserts Babák (1913), "that the nervous system, under the influence of the light relations of the environment, controls not only the movements and the mass of the pigment in the chromatophores, but also influences the division or multiplication of the chromatophores" (*trans.*).

Kuntz (1917) contributed a valuable paper on "The histological basis of adaptive shades and colours in the flounder, *Paralichthys albiguttus*". He reports a reduction of approximately 30% in the number of melanophores in the superficial layer of the dermis when specimens which had been kept for some time on a white background were compared with freshly caught specimens or ones from a black background. This reduction was not so great on a yellow background as upon a white one. It was apparently due to the ejection of melanophores through the skin, a process which takes place normally, though more slowly, in all fishes, regardless of background. A graph which Kuntz presents shows both a decrease in fishes transferred to white backgrounds and an increase when specimens were returned to black. The maximum effect, he found, was attained in 11 days.

The massive contributions of Murisier (1920–1) must be given prominence in any discussion of our present topic. This investigator, working on young trout, found that white and black backgrounds strongly influenced the quantity of melanin produced, without appreciably influencing the growth of the fish. For one experiment, he reports that the mean number of melanophores counted in the dorsal fins of the white-adapted fishes was 295, that for the black-adapted fishes being 680, and for ones kept in total darkness, 330. Corresponding figures for the anal fins were 4, 67 and 5. Murisier believed, however, that whereas sojourn on black leads to a great increase in the number of melanophores, sojourn on white merely causes a retardation of the further production of these cells, not a loss of those previously present. This last conclusion is not in agreement with the findings of most others who have performed similar experiments upon fishes.

The work of Kudô (1922) is sometimes seriously cited in discussions of quantitative pigment changes in fishes. His report as a whole is so unconvincing, however, and his claims so incredible, that I cannot attribute any importance to them. His thesis is that the darkening of a fish, however called forth and apparently of however brief duration, results from an actual increase in the amount of melanin present. Even "Tötung durch Schläge auf den Kopf" produces an increase in this substance. Pictures of test-tubes containing various amounts of dark precipitates are offered as evidence for these effects.[1]

Hewer (1927, 1931), working upon English flatfishes, found that an increase in epidermal melanophores occurred as a result of exposing his fishes for two or three

[1] In a previous paper (1939*a*), I referred to these pictures as not being photographs. I had overlooked a statement in the text: "Die Abbildungen sind direkte Aufnahmen auf Entwicklungspapier, ohne Negativ." Regardless of the process of reproduction of these figures, however, we may doubt whether they are likely to be convincing to anyone who has undertaken the assay of melanin.

weeks to a black background. The numbers both of erythrophores and iridiophores (guanophores) were likewise found to be influenced by the background, the former undergoing an increase on orange and a decrease on white; the latter undergoing an increase on white. Hewer expressed the belief that changes produced in this way through the influence of optic stimuli have a possible evolutionary significance, so that "factors in the environment producing temporary adjustments also produce more permanent effects of a strictly structural character" (1931).

Vilter (1931*a*) reports an experiment in which he endeavoured to assay the melanin content of two axolotls which had been kept on black and white background for a period of 17 months. The method of Piettre (1911) was employed. This consists in grinding up the tissues in a mortar, mixing them with large quantities of water, allowing the debris to settle, decanting, and then centrifuging the overlying liquid, after this has been kept 24 hr. at a low temperature. Vilter states that four times as much melanin was extracted from the black specimen as from the pale one, and offers a photograph showing the two lots of material. Although this method would seem to be far from precisely quantitative, the difference in the yield of the two individuals appears to be sufficiently marked. It is unfortunate, however, that Vilter did not employ larger numbers of specimens in this important experiment.

For some years, the present writer and several collaborators have been experimenting upon the effects of visual stimuli on the production or loss of pigment in certain fishes. It must be explained that our procedures have been changed from time to time, in the course of these experiments, as likewise our mode of presenting the same data to the reader. For this reason, inconsistencies (more apparent than real) would be evident to a reader who should carefully compare the various reports of this work.

In *Lebistes* (Sumner & Wells, 1933) a rather rapid loss of melanin was found to occur, when fishes of "black" history were transferred to a white background. After a few days, it required but low magnification to reveal the presence of numerous degenerating melanophores in the surface of the skin, while in sections, large rounded masses of melanin were seen to be passing to the exterior through the epidermis. This bleaching process lasted for some weeks. Returning such bleached fishes to black containers resulted, in a few days, in the appearance of numerous small pigment masses in the dermis, which increased in number and size for some weeks. These changes were not confined to the skin, however, for wide differences were found in the peritoneum and other regions between individuals of black and white history, as had already been noted by Murisier (1920–1) for the trout and Vilter (1931*b*) for the axolotl. (Vilter reports that the livers of black axolotls contain "enormous" quantities of melanin.)

Even the most prolonged exposure to a given background failed to render the resulting state of the chromatophores permanent. Fishes reared from birth in black or white containers, even when the light was continued night and day, and throughout their entire lives, responded fairly promptly to a reversal of their backgrounds, though not so promptly as ones which had been kept for only a month

upon a given background, after attainment of maturity. This was true, indeed, of some which represented a third generation reared under the conditions stated. These last experiments relate to transitory colour changes, but the same statements would doubtless apply to quantitative ones as well.

Odiorne (1933, 1936) experimented extensively in this field at about the same time that our La Jolla experiments were conducted. He employed fishes of a number of species, chiefly members of the genus *Fundulus*. Like several of his predecessors, Odiorne determined, in some cases, the extent of background influence in terms of the density of chromatophore distribution per unit area of skin. It is of interest that while a loss of melanin upon white backgrounds was everywhere manifest (nearly 60% in 10 weeks, in one case), the occurrence of an increase upon black was far less evident. This, it will be recalled, is the reverse of what Murisier found in the case of the trout. There would seem to be nothing inconsistent, however, in the results of these two investigators. The occurrence of a loss or a gain in pigmentation, and the extent of this, might be expected to depend largely upon the background from which a given fish was taken. With some fishes, at least, it is certainly easy to increase the number of chromatophores in a specimen which has previously been white-adapted, and to decrease the number in one which has been dark-adapted. Odiorne, like some others, notes the occurrence (in *Macropodus*) of internal differences in melanophore abundance between dark-adapted and light-adapted specimens.

Thus far, no endeavour seems to have been made to establish any exact quantitative relations between visual stimuli and the ensuing pigmental modifications. Experiments with this in view were commenced in our laboratory, in November 1935. Results thus far obtained have been reported in several papers (Sumner & Doudoroff, 1937, 1938*a*, 1938*b*; Sumner, 1939*a*, 1939*b*, 1940).

In the first series of such experiments, gobies (*Gillichthys mirabilis*) were employed. These were kept in glass aquaria, painted on the outside with black, white and two shades of grey. Sets of aquaria, thus painted, were exposed to two widely different illuminations, these last being approximately in the ratio of 40 : 1.

After the fishes had been submitted to these conditions for nearly three months, an assay of the melanin was undertaken. This consisted essentially of colorimetric determinations of the dark material left in solution after removal of fats, proteins and bone.

These measurements indicate clearly the existence of a graded series of melanin values, corresponding to the series of shades used as backgrounds (white, pale grey, dark grey, black). Moreover, when these values were plotted against the measured albedos of the background, they assumed a logarithmic rather than a linear arrangement.[1] The rule which we proposed provisionally was that the quantity of melanin produced or lost varied inversely as the logarithm of the albedo of the background. On the other hand, it was found that the intensity of the illumination played but a minor part in bringing about pigmental changes, although the more

[1] This was less true of the figures for the more dimly lighted of the two series.

brightly lighted fishes produced slightly more melanin, except in the case of the white (see below).

Similar experiments were later undertaken with *Gambusia affinis*[1] (Sumner & Doudoroff, 1938*a*). These deserve merely passing notice, owing to considerable and quite unaccountable variations in the yield of melanin from lots of fishes of presumably identical history. It is, however, worth noting that the graphs for the background experiment showed a similar trend to that which was encountered in our gobies, i.e. a more nearly logarithmic than linear arrangement of the values. On the other hand, no significant differences were detected as a result of the widely different illuminations employed.

Measurements of melanin were discontinued at this time, and a new technique substituted, namely, the counting of melanophores in given unit areas of the skin. For this purpose, the "guppy" (*Lebistes reticulatus*) was used. The first of these experiments related to the effects of backgrounds. Five of these were employed: white, three shades of grey, and black. Small aquaria of clear glass were used, painted the required shades on the outside. These aquaria were kept in a cabinet divided into four compartments, each lighted by a 100 W. lamp. Readings both of incident light and of reflexion from the bottoms of the aquaria were made with photo-electric equipment.

About thirty-five female guppies were kept in each of these aquaria for a period of about two months. In this, as in all our experiments, the fishes were well fed throughout the period. In the end, they were subjected to adrenalin, in order to bring about the concentrated state of the melanin, necessary for counting the melanophores. After this, they were fixed, and cleared in cedar oil. A slice was removed from the premaxillary region, and the number of melanophores in a given area of definite position was counted with the aid of a Whipple eyepiece micrometer disk.

Fig. 1 represents the frequency distributions for the various melanin values of fifty specimens of each of the five lots of fishes comprised in this experiment. It is probable that the great variability within each of these lots is due largely to genetic differences in a highly mixed stock of *Lebistes*. The mean differences in melanophore number between these various lots, although considerable, are not so great as might have been expected in view of the widely different appearance of these fishes in life. The mean number found in the "black" fishes, for example, is less than three times as great as that for the "white" ones. It is evident that a large part of the visible difference of shade among these fishes is due to factors other than the number of melanophores. Some of it is due to the melanin content of the individual melanophores; much of it, of course, to the state of aggregation or dispersion of the melanin. Fig. 2 is based upon the mean values of the five series represented in Fig. 1. It shows the relations between the number of melanophores per unit area and the albedo of the background on which the fishes were kept. The albedos have been reduced to percentages of the albedo of the white background, taken as 100. The

[1] Owing to misinformation, I referred to this same species earlier (Sumner, 1935) as *Gambusia patruelis*.

numbers given for the melanophores are multiples of the mean number for the "white" fishes taken as unity.

The form of this curve obviously suggests a logarithmic relation between the two sets of values. Fig. 3 shows that this relation holds fairly closely for all of these lots of fishes with the exception of those for black. It would be necessary either to raise the albedo from 0·74 to about 2·0, or to raise the melanophore index from 2·55 to about 3·0 in order to bring the "black" fishes into line.[1] It is plain, nevertheless, that the relation between the two variables, albedo and melanin production, is much more nearly a logarithmic than a linear one. This relationship is of considerable theoretical interest as will be pointed out below.

(2) *Guanin*

The pigmental effects thus far considered have related solely to the black substance melanin. It has been observed by several investigators (Kuntz, 1917; Murisier, 1920–1; Meyer, 1931; Sumner & Wells, 1933) that decrease in the production of melanophores, in white-adapted fishes, is accompanied by a marked increase in the number of guanophores, or at least in the amount of visible guanin. No quantitative determinations of the latter substance have, however, been reported.

Meyer (1931) states that she undertook such determinations, though she has not indicated her procedure.

(3) *Carotenoid pigments*

Šecérov (1909) reports "morphological colour changes" in coloured pigments as well as black in *Nemacheilus*. Since, however, he speaks of finding "red, reddish brown, green, greenish, greenish yellow and orange coloured pigments", as well as black and yellow ones, in this fish, his reports regarding pigments must be taken with considerable reservation.

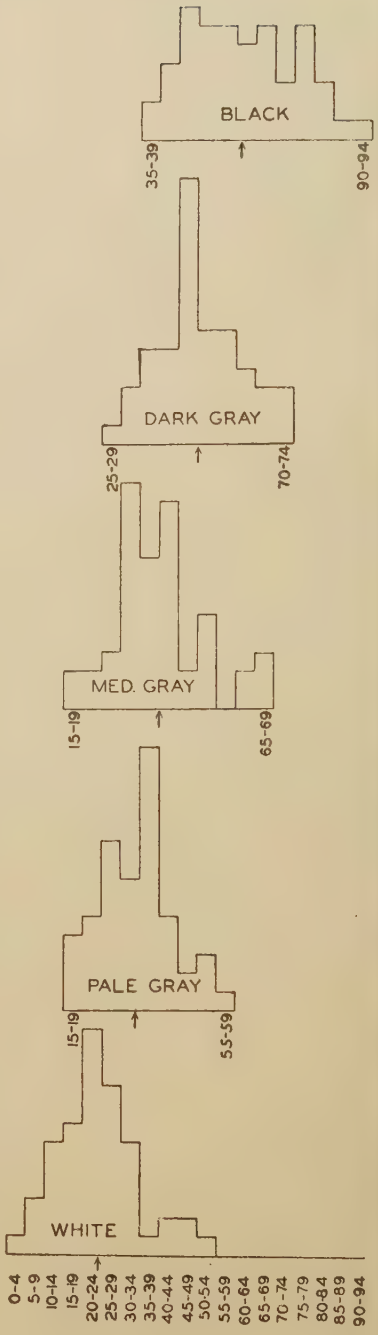


Fig. 1. Frequency distributions of the number of melanophores in a definite area of the premaxillary region of *Lebistes*. Based upon 50 individuals from each of the five backgrounds.

[1] In a recent paper (Sumner, 1939*a*), I provisionally assigned to the black background an estimated value of 2·0, there being, at that time, no available means of determining its exact value. In a graph (Fig. 5) this provisional value was unfortunately included.

Kammerer (1913), after an extended series of experiments, reported not only that young salamanders (*Salamandra maculosa*) responded by quantitative pigmental changes to different backgrounds (black and yellow) but that these changes were ultimately inherited. Even the former of these contentions was disputed by Herbst (1919, 1924), who repeated Kammerer's experiments upon the same species. Herbst reared his specimens from birth to an age of several years. He found that during the larval stages the yellow spots increased in relative size in animals kept upon yellow backgrounds and decreased in those kept upon black ones. After metamorphosis, however, the reverse tendency was manifest, leading to a con-

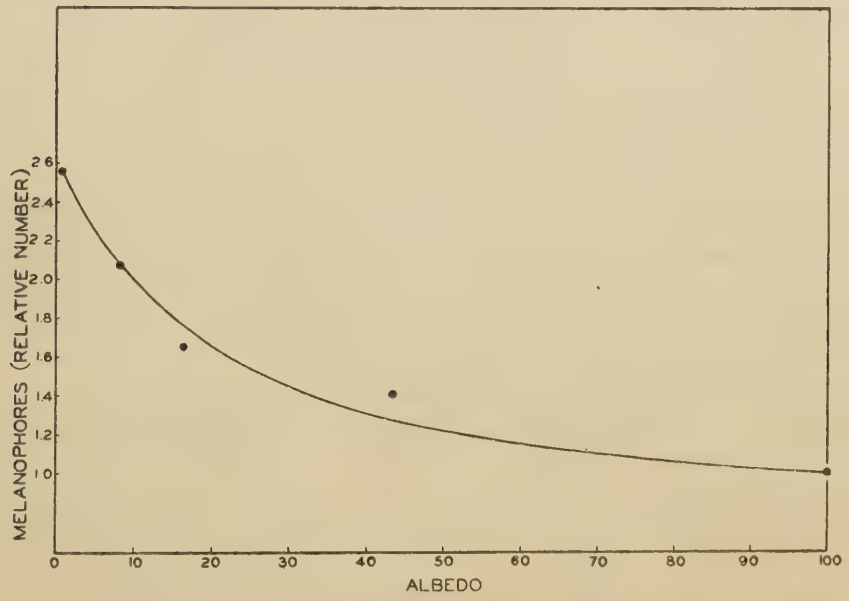


Fig. 2. Relations between albedo and melanophore density, based upon the same individuals as Fig. 1. Abscissas = albedos of the five backgrounds, taken as percentages of that for "white", regarded as 100. Ordinates = mean values for the five lots of fishes, reduced to multiples of the mean value for the "white" fishes.

vergence of the two lots in respect to their colour characters. Since Kammerer started his experiments with post-larval individuals, Herbst believed that he had refuted Kammerer's claims. On the other hand, these claims of Kammerer, as regards the first generation, were confirmed by von Frisch (1920), who concluded that the difference between Kammerer's results and those of Herbst were the results of differing experimental conditions.

Mast (1916), referring to his experiments in which flatfishes were raised on coloured backgrounds, states that "on the reds, greens, and blues adaptive changes still appear to continue after a sojourn on them of between two and three months". Although Mast does not suggest that any quantitative changes in pigmentation occurred on such occasions, the duration of these changes renders it probable that this was the case.

The experiments of Hewer (1927, 1931) may be recalled (see above), since they involve coloured pigmentation as well as black. No determinations appear to have been made by any of these writers, however, either of the number of chromatophores or the quantity of pigment.

The studies of Sumner & Fox (1933, 1935*a*, 1935*b*) relate to quantitative changes in yellow pigment of the xanthophyll series. Fishes of several species (*Fundulus parvipinnis*, *Gillichthys mirabilis*, *Girella nigricans*) were employed in these studies, the xanthophyll being extracted with customary solvents and the resulting solutions assayed colorimetrically. While all these fishes were found to respond in an imitative fashion to yellow backgrounds, as well as to black, grey and white ones, it is of interest that out of the three, *Girella* alone manifested any differences in the actual amount of yellow which it yielded. It is interesting, too, that the amount of xanthophyll present (though not the visible appearance of the fish) appeared to depend upon the shade (whether light or dark), rather than upon the colour (spectral value) of the background. Thus, the greatest amount of xanthophyll was extracted from the almost inky black fishes which had been kept on black, the least from fishes kept on white, while intermediate and nearly equal amounts were yielded by specimens kept on a rather rich yellow and upon a neutral grey of medium shade. It should be added that *Girella*, in all circumstances (though not *Fundulus*), was found to lose xanthophyll under laboratory conditions. The relations stated above indicate, therefore, relative rates of loss.

Incidental, only roughly quantitative, determinations were made of the xanthophyll content of the fishes in certain later experiments (Sumner, 1940). Striking differences were noted in the colour of the 95% alcohol to which the fishes were subjected at one stage of their preparation. In the first of these experiments, in which five backgrounds were used (black, three greys and white), it was obvious that the alcohol from the "black" fishes was by far the most highly coloured (yellow) of any of this series, while that from the "dark grey" ones rated second. The three other lots did not differ appreciably in this respect.

In the second experiment, in which only two types of background (black and medium grey) were employed, the extracts from the "black" fishes were more deeply coloured than those from the "grey" ones at all four intensities of overhead illumination, the latter factor having little or no influence in the matter. In comparisons made with Nessler tubes, it was found necessary to dilute the xanthophyll solution from "black" fishes to 25% of its original strength in order that it should approximately balance that from the "grey" fishes.

In our studies of carotenoid pigments, no attempt was made to count xanthophores, nor were any microscopic studies made. Abramowitz (1935), however, examined and counted xanthophores in the caudal fin of *Fundulus majalis*, before and after keeping the fishes on black, white, yellow and blue backgrounds. After periods ranging from 12 days to 6 weeks, increases were noted on yellow and black, decreases on blue and white.

III. INTENSITY OF ILLUMINATION

Investigators early discovered that the responses of poikilochromic animals to their backgrounds were, within wide limits, independent of the intensity of the incident light. That this is not absolutely true, however, has been likewise recognized. Brown (1936) has recently shown that at certain very low light intensities, in fishes kept upon identical backgrounds, "the average diameter of pigment masses is directly proportional to the logarithm of the light intensity". Brown was not concerned here with the quantity of melanin present but with the relative degree of expansion or contraction of the pigment masses within the melanophores.

In discussing the goby experiments of Sumner & Doudoroff (1937), I have already pointed out that the more brightly lighted fishes produced on the whole slightly more melanin than the less brightly lighted ones. This was not true, however, of the fishes in white aquaria, in which the amounts were nearly equal, and indeed the relation did not seem to be clearly established in any case. In the much less satisfactory *Gambusia* experiment (Sumner & Doudoroff, 1938*a*), any such difference was even less probable.

It seemed highly desirable to test more precisely the part which was played, if any, by light intensity in influencing the production or elimination of melanophores. This was undertaken in one of the experiments with *Lebistes* (Sumner, 1940). The degrees of illumination received by the aquaria, in the four compartments of the cabinet here employed, were approximately 64, 5·3, 0·85 and 0·24 foot-candles respectively. Special steps were taken to keep the temperature in these compartments approximately equal.

Although the primary object of this experiment was to test the possible effects of light intensity, aquaria of two shades (black and medium grey) were used with each degree of illumination.

When the mean values for fishes from these four compartments were computed, a steady, though slight increase in pigmentation was shown in passing from the lower to the higher illuminations. However, there is little consistency in this respect when the figures for the two backgrounds are considered separately. Moreover, the single differences are of little statistical significance. Nevertheless, the differences are in the same direction as those shown in the earlier experiment by Sumner & Doudoroff (see above). The absence of any obvious effect of light intensity upon xanthophyll formation in this experiment has already been pointed out.

As the limiting case in our discussion of light intensity, we may consider the effect of total darkness upon pigmentation. It is noteworthy that fishes and Amphibia, whether normal or blinded, have usually been found to become pale when kept in the dark, and in a few of these cases the amount of pigment is said to have been involved (Ogneff, 1908; Babák, 1913; Murisier, 1920–1; Odiorne, 1937). Murisier found that the number of melanophores, per unit area of the skin, in young trout which were kept in the dark, was little greater than in specimens which had been kept upon a white background in the light, though the melanophores were less than half as numerous as in specimens kept upon a dark background. Odiorne reports

similar, though less marked, changes in *Fundulus*. This somewhat surprising effect of darkness upon the chromatophores has been offered as a possible explanation of the depigmentation of cave animals (Ogneff, 1908).[1]

IV. BLINDING

Although the pigmental conditions of blinded fishes can hardly be attributed to *optic* stimuli, they may be fairly credited to the withdrawal of these stimuli, or at least to the withdrawal of impulses proceeding from the retina. But whereas total darkness results, as we have seen, in a process of depigmentation, blinding, in the presence of light, results in a marked increase of pigmentation.

Mayerhofer (1909) reported a great increase in the pigmentation of blinded pike (*Esox*) when kept in the light. The lateral dark bands extended themselves downward until large areas of the normally white ventral area were covered with melanophores. This effect did not ensue when the fishes were kept in the dark. Similar results were reported by Šecérov (1909) for *Nemacheilus*.

Von Frisch (1911) recorded a much less convincing case for the trout. After determining the interesting fact that the removal of one eye in this fish caused a functional darkening of the opposite side of the body, he attempted to determine the relative density of the chromatophores on the dark and pale sides. He counted a slightly greater number of these cells per unit area for the darker side, but this difference was not statistically significant. Babák (1913) reports a great increase in visible pigment in blinded *Amblystoma*, kept in the light. This depended in part upon an increase in the number of chromatophores, following an enormous extension of their contained pigment masses. Fischel (1920) obtained similar results, likewise with *Amblystoma*. He called attention to the formation of an immense syncytium of melanophores, covering the entire body, except for the yellow spots. This increase in the black pigmentation extended to some internal parts. Murisier (1920–1) found that blinded trout became even more heavily pigmented than normal fishes kept upon a black background. Similar results have been reported by Giersberg (1934) for the goldfish and by Odiorne (1937) for *Ameiurus*. I myself have obtained confirmatory results in experiments upon *Lebistes reticulatus* (unpublished), though no counts or measurements were attempted in this case. I also found, in agreement with Fischel, that some of the blinded specimens grew to an exceptionally large size.

Since numerous writers have pointed out that blinded fishes soon become dark when well lighted, we should expect them to acquire heavier pigmentation, in accordance with the accepted principle (see below) that transitory colour changes, if prolonged, lead to quantitative ones.

V. DIRECT ILLUMINATION WITH COLOURED LIGHT

Various investigators have studied the effects of coloured (more or less monochromatic) light upon fishes. Šecérov (1909) performed such experiments, but his results are open to doubt for reasons stated above. Moreover, von Frisch (1911)

[1] It is uncertain to what extent Ogneff attributed this effect to darkness *per se*, and to what extent to diminished food supply.

failed to confirm some of his findings. The results reported by the latter writer, however interesting, relate only to transitory changes and call for no discussion here.

The experiments of Kurz (1920) are more relevant. He exposed the eggs and larvae of *Pleuronectes* and *Esox* to white light, total darkness, and to light of five different colours. No effects were observed in the case of the pike, after three months' exposure to these conditions. For the flounders, on the other hand, Kurz reported certain effects upon the further development of pigment cells once produced, though not upon their origin. White and short-waved light, he states, further the development both of black and coloured pigments; red, yellow and green retard the development of both. Complete darkness strongly retards the development of black and completely suppresses the development of coloured pigments.

VI. ILLUMINATION FROM BELOW

The well-known experiments of Cunningham upon flatfishes should be mentioned among the possible effects of optic stimuli, although it appears to have been believed by that author that the increase in pigmentation which he observed was due to the direct action of light upon the skin (Cunningham, 1893, 1895; Cunningham & MacMunn, 1893). Cunningham placed young flatfishes in glass-bottomed aquaria, illuminated from below by mirrors. At the end of many months, some of these specimens developed extensive pigmented areas, containing both black and yellow chromatophores, upon the lower, normally uncoloured side of the body. These abnormally situated chromatophores were said to undergo colour changes like those which may be called forth on the normal upper side of the body.

It is uncertain, however, that this unusual development of pigmentation was due to the direct action of light upon the skin. The not very precise account of the actual visual fields of these fishes leaves it possible to suspect that the effects were due to the optical conditions of the experiment, as has been suggested by Odiorne (1937). The actual nature of the field of vision of an animal, when placed some distance above a mirror, is not very obvious. On first thought, one might assume that the lower portion of this field was a uniform, well-lighted area, optically equivalent to an extended white surface; but a little observation shows that this cannot ordinarily be the case. So far as I have observed, too, a fish's immediate reaction, when suspended over a mirror, is very different from its reaction when placed in a white-bottomed dish. In the former case, far from becoming pale, the animal becomes dark or fairly so. This would suggest that the effects of any particular type of illumination upon "physiological" colour change should be carefully ascertained before we attempt to interpret its effects upon pigment production.[1]

The experiments of Herbst & Ascher (1927) were of a similar nature to Cunningham's and are, I believe, subject to the same comment. These authors placed larvae of *Salamandra maculosa* in small, glass-bottomed aquaria, which were covered on the sides and above with opaque materials. Mirrors reflected light from

[1] See, however, Addendum.

below. The salamanders were kept for from 4 to 7 years (!) under these conditions, controls being kept in black-bottomed containers, lighted from above. While the relative extent of the spotted areas underwent little change, there was a marked increase in the intensity of pigmentation on the animals' ventral surfaces. Not only melanin, but the lipochrome (carotenoid) pigment and guanin were all found to have increased. These writers appear to assume that the effects in question were due to the direct action of light upon the chromatophores, and this, of course, may be the correct interpretation, though it is by no means certain.

VII. SOME IMPLICATIONS OF THE RESPONSE TO BACKGROUND

Evidence has been offered for the conclusion that in fishes kept for considerable periods on various backgrounds, the amount of melanin (or the number of melanophores) varies inversely as the logarithm of the albedo of these backgrounds. This conclusion is of considerable theoretical interest. The analogy has been pointed out (Sumner & Doudoroff, 1937; Sumner, 1939*a*, 1939*b*) between these pigmental relations of fishes and those phenomena of human sense perception upon which the "Weber-Fechner Law" was based. Even the downward displacement of the melanin value for the "black" fishes (Fig. 3), as compared with its "expected" value, might be regarded as giving additional support to this analogy. As is well known, the Weber-Fechner rule, so far as it relates to visual stimuli, breaks down in the realm of feeble intensities, greater relative increments of stimulus being required in order to bring about perceptible increments of sensation. Whether this deficient (even if actually very high) production of melanin upon a background of very low albedo can be regarded as comparable with the human case is, of course, far from certain. But the coincidence is at least suggestive.

Considerable evidence has also been presented which shows that shade of background is a much more potent factor than intensity of illumination in determining the pigmentary response of the animal. From the viewpoint of a fish or amphibian, as has already been remarked, the difference between incident light and background is a purely topographic one, the upper portions of the visual field rating as "incident light", the lower portions as "background". The albedo of a background, as defined earlier, is the ratio between the light which it receives and the light which it reflects. Response to albedo, therefore, would seem to be determined by the relative degrees of illumination of the upper and lower portions of the retina. This "ratio" theory of an animal's response to the shade of the background, and the correlative assumption of a differentiation of functions in different parts of the retina, have received increasing attention in recent years. Although previous discussions have related wholly to colour changes of the transitory type, we may be certain that the phenomena in question extend to quantitative changes as well.

In reviewing briefly some of the investigations which bear upon the relations indicated, we may distinguish discussions of (1) the "ratio theory", and (2) the functional differentiation of the retina, although it is evident that these two conceptions are closely interconnected. The former appears to have first been clearly stated by Keeble & Gamble (1904) for certain crustaceans. The same formulation

was independently made by myself (1911) as a result of experiments upon flatfishes, though no specific test of the theory was then undertaken. Mast (1916) undertook such an experimental test, likewise with flatfishes. His results were partially confirmatory, though in some respects inconclusive. What seemed to be a critical demonstration of the proposition was made by Sumner & Keys (1929) by the use of an apparatus which made it possible to brighten or darken the background, to some extent independently of the overhead illumination. These findings were confirmed for young catfish by Pearson (1930), by the use of similar methods, though Pearson

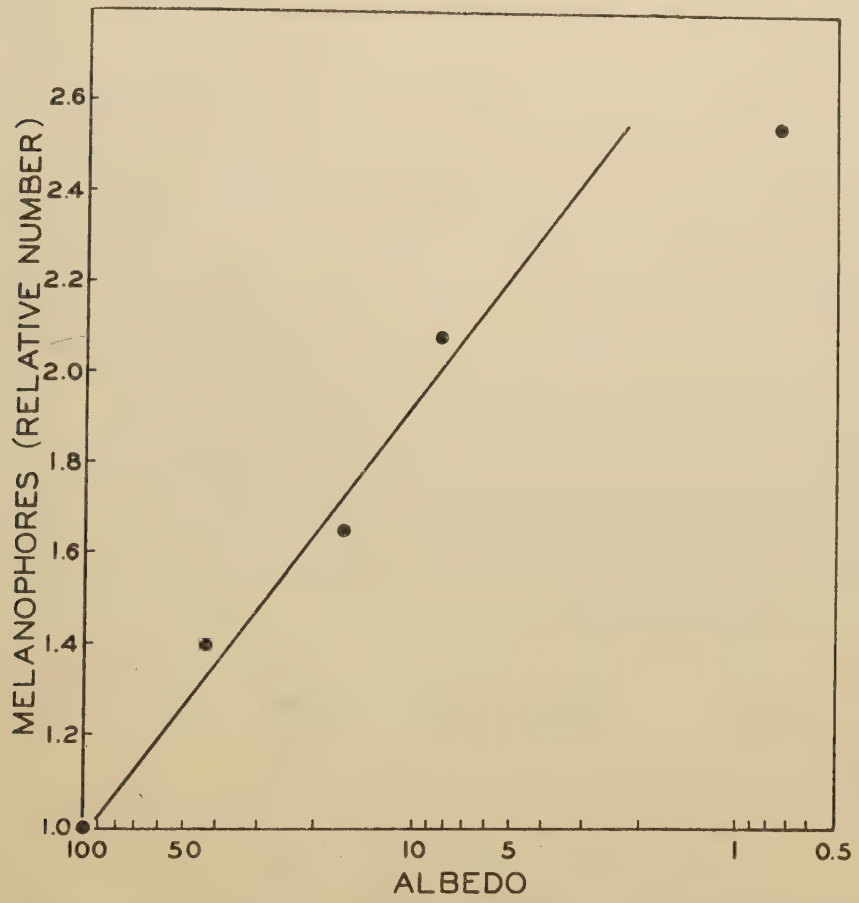


Fig. 3. Same values for melanophores as in Fig. 2, plotted against the logarithms of the albedos.

has insisted upon the limited range within which the rule holds. Brown (1936), using more exact quantitative methods, corroborated the "ratio theory" for the fish *Ericymba buccata*, except for very low light intensities. Butcher (1939) has carried out an intensive series of experiments with *Fundulus* (presumably *F. heteroclitus*), in which varying relations were maintained between the light intensities above and below the fish. Butcher concludes that "The shade assumed by *Funduli*, therefore, depends upon the ratio between the direct and the reflected light entering the eye".

Conclusions relative to a functional differentiation of different portions of the retina have been reached by a number of writers, not all of whom have been concerned with the "ratio" theory of response to background. Suggestions to this effect have been made by Schnurmann (1920), Meyer (1931), Hogben & Slome (1936), and Vilter (1938).

Von Frisch (1911), Parker & Lanchner (1922), Sumner (1933), Butcher & Adelmann (1937) and Butcher (1938) have employed the method of screening the whole or portions of the eye with opaque materials. Sumner, Butcher and Adelmann agree that stimulation of the upper and lower halves of the retina have opposite effects. Other factors remaining constant, the illumination of the upper half leads to a paling of the fish, while illumination of the lower half leads to a darkening. Conversely, darkening the upper half of the retina leads to a darkening of the fish, while darkening of the lower half leads to a paling. Von Frisch (1911) had observed the darkening effect of covering the lower half of the cornea for brief periods (i.e. shading the upper half of the retina), but he believed that covering the upper half of the cornea led to no result.

Several writers have performed the experiment of rotating the eye of a fish in its socket through 180°, thus reversing the normal relations of the retina to the visual field. Sumner (1933) obtained no instructive results from this procedure, owing to the serious (ultimately fatal) effect of the operation upon the fishes. Butcher & Adelman (1937) and Butcher (1938) report success in a number of cases, with results which conform to expectations based upon the results of their other experiments. Butcher accepts the "ratio" theory with some modifications. Vilter (1937, 1938) reports success in rotating the eyes of the axolotl. There ensues, he says, an inversion of the dorso-ventral differentiation of the skin pigmentation, the ventral surface darkening and the dorsal surface paling. Vilter states, however, that such an "inverted" specimen darkens upon a dark bottom, as well as a normal specimen. He offers an explanation based on the respective roles which he attributes to nervous and the hormonal control of the chromatophores.

It may be well to repeat that none of these experiments relative to functional differentiations of the retina have had in view the production of quantitative pigmental changes.

VIII. THE RELATION BETWEEN "PHYSIOLOGICAL" AND "MORPHOLOGICAL" COLOUR CHANGES

Although we are not concerned here with invertebrates, it is worth noting that Keeble & Gamble (1904) recognized the activity of the crustacean chromatophores in "manufacturing and storing or transforming pigmentary substances", through the mediation of the eyes and nervous system.

Babák noted many years ago (1910, 1912, 1913) that prolonged "expansion" or "contraction" of chromatophores led to quantitative changes in these. With respect to this fact, he offered the following explanation (*trans.*): "We can comprehend all these phenomena consistently if we suppose that the continued expan-

sion of the chromatophores [however brought about] so alters the nutritive condition of the pigment cells that not only an increase of pigment will be brought about in the latter, but also favourable conditions for rapid division, i.e. for chromatophore multiplication, will be produced. On the contrary, the continued contraction of the chromatophores [however brought about] is bound up not only with weaker pigment formation, or even pigment reduction, but also with the checking of the nutritive processes leading to the division of the pigment cells." Babák points out the ecological significance of this identity between conditions which call forth "expansion" of the chromatophores and ones which call forth a permanent increase in the amount of pigment, and conversely with "contraction".

This recognition of the causal relation between the phenomena of transitory and of quantitative colour change has been called by more than one writer "Babák's Law". Stated merely as a causal relation, it is now generally accepted by workers in this field. It appears to be uncertain, however, whether the states of chromatophore "expansion" and "contraction" directly cause the trophic conditions which lead to the multiplication or elimination of these cells, as Babák, Himmer and Giersberg believe, or whether these are merely parallel results of a common (perhaps hormonal) cause, as was admitted as a possibility by Giersberg, and has recently been maintained by Odiorne.

Himmer (1923) set out to test Babák's contention that "morphological" colour changes are a result of prolonged "physiological" colour changes. He performed the interesting experiment of subjecting larval salamanders to dilute solutions of cocaine, a substance which he found to produce a continued state of contraction of the melanin masses, regardless of any visual stimuli. The result was a reduction in the number of melanophores, a condition which was limited, however, to the larval stages. Neither xanthophores nor guanophores were affected by this treatment.

These results would seem to favour the view that the quantitative reduction of melanin is a direct effect of its being concentrated within the cell. But such observations as Himmer's plainly demand confirmation.

Murisier (1920–1) does not appear to be altogether consistent in his statements on this question. At one point, he expresses the belief that "the contraction of the melanophores arrests the elaboration of their pigment and retards their augmentation in number". Later, however, he states: "The inhibition of pigmentogenesis does not result then from the accumulation of pigment at the centre of the cell, since it already manifests itself in the pre-pigmentary element, before the appearance of melanin granules. One arrives thus at the idea that the centripetal migration of the pigment granules and the arrest of pigmentogenesis represent two parallel but secondary effects of the same primordial cause: the arrest of nutrition of the cell which elaborates the melanin." (*trans.*)

Giersberg (1934) also hesitates between the view that "morphological" colour change is the direct result of "physiological", and the view that both are the result of a common hormonal cause. He concludes that neither relation need hold in all cases. As evidence that a continued "contraction" of the melanophore pigment may result in its diminution, he points, among other things, to the outcome of an

experiment in which he injected a young brown goldfish with adrenalin throughout a period of 1½ years. As a result, this animal ultimately lost its yellow and brown pigments. He suggests, furthermore, that the loss of pigment in a fish kept on a white background is due to the secretion of adrenalin into the blood. Such an experiment as the one cited certainly demands repetition. Furthermore, if this result were confirmed, one might still be very doubtful whether loss of pigment following sojourn upon white is due to the same cause.

Odiorne (1936) expresses unequivocally the view that "morphological colour changes (alterations in pigmentation) and physiological colour changes (arising from pigmentary movements) are phenomena resulting from a common cause. The former are not regarded as dependent upon the latter.... The neurohumors which are instrumental in bringing about the pigmentary migrations in *Fundulus* also exert trophic influences upon the melanophores."

This last view accords better with our present knowledge of the "neurohumoral" action of pigmentomotor nerves as developed by Parker and others. It accords better also with the fact that numerous chromatophores may appear in a fish undergoing black adaptation, which do not seem to arise from pre-existing chromatophores (Murisier, 1920–1; Sumner & Wells, 1933).

IX. NERVOUS AND HORMONAL CONTROL OF CHROMATOPHORES

The question of the mechanism by which stimuli originating in the retina are transmitted to the effector organs, the chromatophores, is only incidental to the primary object of this review, though it is probably the aspect of colour-change physiology which is receiving the greatest attention at the present time.[1] An increasing role is being assigned to hormones in linking the receptor with the effector organs. These are partly well-recognized hormones from endocrine glands (pituitary and adrenal), which may be transmitted through the blood stream in response to retinal stimulation, partly a more hypothetical class of "neurohumors", which seem to be generated at the sympathetic nerve terminals and to diffuse through the tissues. Hormonal control has thus far been studied almost wholly in relation to the transitory "physiological" colour changes, though it is likely that quantitative changes result in time from any influence which brings about the transitory ones.

Pouchet (1876) demonstrated experimentally the control of the chromatophores in teleost fishes through the sympathetic nervous system, and Ballowitz (1893) furnished what seems to be conclusive histological evidence of the intimate connexion between these cells and the nerve terminals. Indeed, with certain modifications, the hypothesis of direct nervous control appears to be universally accepted at the present time for the teleost fishes.

The modifications have been in two directions. (1) Numerous experiments have shown that responses to visual stimuli may occur, though tardily, after this intimate connexion between the nerve fibrils and some particular group of chroma-

[1] Rather extensive bibliographies of this phase of the subject have been given by Parker (1930, 1932, 1936, 1938), who, along with a considerable group of collaborators, has been an outstanding leader in this field during the past two decades.

tophores has been abolished. This has led to the supposition that even in "direct" nervous control, the responses are due to hormones liberated at the nerve terminals and carried to the chromatophores by intercellular diffusion (Meyer, 1931; Parker, 1934*a*; Giersberg, 1934; Veil, 1936; and others).

(2) Evidence has been offered, tending to show that even in teleosts a certain amount of influence may be exerted by blood-borne hormones (chiefly those of the pituitary), which are liberated in response to various stimuli (visual among others), and act directly upon the chromatophores, independently of any local nervous control (Parker, 1934*b*; Giersberg, 1934). So far as teleosts are concerned, such a process is generally believed to be of secondary importance, as compared with more direct forms of nervous control. The blood-borne hormone here involved is usually presumed to be a product (or products) of the pituitary. But Giersberg (1934) has suggested that adrenalin may likewise be liberated into the blood stream, in fishes undergoing white adaptation. It is further contended by Giersberg (1930, 1932) that the coloured chromatophores (lipophores) of the minnow, *Phoxinus*, are not innervated at all, but are regulated entirely by the pituitary secretion infundin. Waring (1936) states that "Zondek & Krohn (1932) have shown that in teleosts, injections of posterior lobe pituitary cause an actual increase in the amount of melanin per chromatophore". This is an interesting result and should be confirmed.

An incidental result of possible importance in this connexion was obtained by Sumner & Doudoroff (1938*b*). In the experiments with *Gambusia*, already discussed (p. 357), in which the fishes were kept for considerable periods upon backgrounds of differing albedo (five shades in one experiment, two in another), it was found that the incidence of a fatal disease was far heavier in the black aquaria than in those of lighter shade. In the first experiment, indeed, nearly twice as many fishes died on black as on the other four shades combined. In this experiment, moreover, the death-rate in the dark grey aquaria rated next to that in the black. The figures from the second experiment revealed no probable relation between the incidence of this disease and the intensity of the illumination. As in the case of melanin production, the determining factor was the background. It is, of course, impossible to say whether these differences in morbidity resulted from the changes of pigmentation *per se*, or from physiological processes underlying these changes. It is, however, easier to suppose that physiologically active substances such as hormones could bring about these results than relatively inactive substances such as melanin or xanthophyll.

In elasmobranchs, the evidence for hormonal control seems to be much clearer. Darkening appears to be due to a water-soluble, blood-borne secretion from the hypophysis. Concerning paling, the evidence appears to be contradictory, or perhaps the situation is different in different species. Direct nervous control has apparently been demonstrated in at least one case (Parker & Porter, 1934), while this has not been found in a number of others. Hogben (1936) postulated the existence of a chromatophore-"contacting" secretion in some elasmobranchs, along with the "expanding" secretion from the pituitary. So far as I know, no quantitative pigmental changes have been recorded for fishes of this group.

It is in the Amphibia that the hormonal control of the chromatophores has been longest and most widely recognized. In this group, colour change appears to be chiefly if not wholly controlled by that means. The effect of extirpating the hypophysis upon the visible pigmentation of amphibian larvae was early shown by Smith (1916) and Allen (1917). The former reported an extensive loss of the black pigment.

Hogben concluded, after a summary of existing knowledge in this field (1924), that "the hypothesis of pituitary secretion fluctuating in correspondence with the action of natural stimuli tending to produce colour response is in the existing state of knowledge adequate, at least in adult Amphibia, to interpret all the salient facts"; and again, "even if a nervous mechanism for regulating colour control exists, it plays no significant role in the rhythm of normal colour response in the Amphibia". Paling, according to this view, results from an inhibition of the secretion of the darkening hormone of the pituitary. More recently, Hogben & Slome (1936) have offered evidence for the existence of both darkening ("B") and paling ("W") substances in the secretion of this gland. It may be said that at present the prevailing view is to the effect that direct (i.e. local) nervous control of the chromatophores is lacking in Amphibia. However, this view is not unanimous.

Vilter (1935, 1938) has recently urged that the control of colour change in the axolotl is "neuro-endocrinienne", specifically "sympathico-hypophysaire". The sympathetic control is inhibitive, tending to "contract" the melanophores and depress their growth and multiplication. Some action of a spatially restricted nature is necessary, he urges, to account for the melanophore patterns in the skin (spotting, and the dorso-ventral contrast in pigmentation). These patterns, at the outset, are said to be purely functional appearances, due to the localized "contraction" of the melanophores. Vilter regards this nervous control as actually being hormonal, however, in the sense of its acting through diffusion hormones, as discussed above. Grafting experiments are offered as evidence of this.

In contrast to the sympathetic control, control by the hypophysis is uniform in its incidence throughout the body; it is melanophore-"expanding" and growth-promoting.

Vilter is disposed to extend his belief in the opposing activities of the hypophysis and sympathetic system to all vertebrates. He cites pathological cases of pigment production, following damage to the sympathetic nerves, and goes so far as to assert that "all natural pigmentation is due to the activity of the hypophysis" (*trans.*).

X. SUMMARY

Fishes and, in lesser degree, Amphibia respond to backgrounds in such a manner that their shade, and to a certain extent their colour, tend to conform to that of the substratum on which they lie, or over which they swim. The integrity of the eyes and of major portions of the nervous system is essential to these phenomena.

The immediate, transitory or "physiological" colour changes are due to the rearrangement of pigment particles already present. When the effective stimuli are

continued for some days or weeks, changes become evident both in the number of chromatophores and in the pigment contents of each (quantitative or "morphological" colour changes).

All three of the types of chromatophores (melanophores, guanophores, lipophores) are affected by these changes. Dark backgrounds favour the production of melanin and inhibit the production of guanin. Pale backgrounds have a reverse effect. In fishes at least, production (or retention) of the yellow pigment xanthophyll is favoured by black backgrounds and retarded by white ones, agreeing thus with melanin. To what extent there is any specific effect of *coloured* backgrounds (*sensu stricto*) upon the quantity of xanthophyll is not clear at present.

Intensity of illumination, above a rather low level, has very little effect upon pigment formation in fishes. There is some evidence, however, of a slight degree of positive correlation between light intensity and melanin formation. Total darkness leads to pigment reduction both in fishes and Amphibia.

Blinding of both eyes, in both of these groups, results in a marked increase of melanin, but only in animals which are kept in the light.

Experiments involving illumination from below are known to have resulted in considerable increases in pigmentation of the ventral surface, both in fishes and Amphibia. It is not certain in these cases whether optic stimuli have been concerned, or whether the effects have been due to direct illumination of the skin.

The response of a fish to its background is primarily a response to albedo, this being defined as the proportion of incident light which is reflected or dispersed from a given surface. On the basis of considerable evidence, a rule has been formulated which has been found to hold approximately, at least for certain fishes. This rule is that, when the animals are subjected to a variety of backgrounds, under uniform illumination, the amount of melanin (or the number of melanophores) produced varies inversely as the logarithm of the albedo of the background. The close analogy between these pigmentary responses of fishes, and the phenomena of sense perception in man for which the "Weber-Fechner Law" was formulated was pointed out.

The question of how a fish recognizes, and responds to, a given albedo, regardless of the absolute degree of illumination present, resolves itself into the question as to how the animal perceives the ratio between the source of light and the light reflected from the bottom and surrounding objects. This last does not seem to be so difficult an achievement when we consider that the ratio in question is ordinarily that between the upper and lower halves of the field of vision, or in other words, between the stimulus received by the lower and upper halves of the retina. Experimental evidence is accumulating showing that these two areas of the retina are functionally differentiated in the required manner.

It was early recognized that those conditions which tend to bring about transitory colour changes are the same ones which, if prolonged, produce quantitative changes. The question has been raised whether the state of chromatophore "expansion" (pigment dispersal) *per se*, promotes pigment production and cell multiplication, and chromatophore "contraction" promotes the reverse processes, or

whether both transitory and quantitative changes are the results of a common (probably hormonal) cause. The weight of present evidence probably favours the latter interpretation.

The relative roles of direct nervous control of the chromatophores and control through hormones is still a subject of controversy, both for fishes and Amphibia. It now seems probable, not only that these two classes of animals differ from one another in important ways, but that the two major groups of fishes, elasmobranchs and teleosts, likewise differ from one another. Even within the group of elasmobranchs, moreover, important differences have been claimed. The whole subject is further complicated by the discovery that "direct" nervous control is itself probably mediated through hormones liberated by the nerve terminals. In general, it is now believed that nervous control (with the reservation just indicated) is the one chiefly involved in the colour changes of teleosts, while control through blood-borne hormones is chiefly involved in the colour changes of both elasmobranchs and Amphibia. But this statement oversimplifies the present state of the problem.

XI. REFERENCES

ABRAMOWITZ, A. A. (1935). "Degeneration of xanthophores in *Fundulus majalis*." *Proc. nat. Acad. Sci., Wash.*, **21**, 132–7.

ALLEN, B. M. (1917). "Effects of the extirpation of the anterior lobe of the hypophysis of *Rana pipiens*." *Biol. Bull. Wood's Hole*, **32**, 117–30.

BABÁK, E. (1910). "Zur chromatischen Hautfunktion der Amphibien." *Pflüg. Arch. ges. Physiol.* **131**, 87–118.

—— (1912). "Ueber den Einfluss des Nervensystems auf die Pigmentbildung." *Zbl. Physiol.* **25**, 1061–6.

—— (1913). "Ueber den Einfluss des Lichtes auf die Vermehrung der Hautchromatophoren." *Pflüg. Arch. ges. Physiol.* **149**, 462–70.

BALLOWITZ, E. (1893). "Die Nervenendungen der Pigmentzellen." *Z. wiss. Zool.* **56**, 673–706.

BROWN, F. A. (1936). "Light intensity and melanophore response in the minnow *Ericymba buccata* Cope." *Biol. Bull. Wood's Hole*, **70**, 8–15.

v. BUDDENBROCK, W. (1928). *Grundriss der vergleichenden Physiologie.* Berlin 830 S. (*Physiologie des Farbwechsels*, pp. 388–412.)

BUTCHER, E. O. (1938). "The structure of the retina of *Fundulus heteroclitus* and the regions of the retina associated with the different chromatophoric responses." *J. exp. Zool.* **79**, 275–97.

—— (1939). "The illumination of the eye necessary for different melanophoric responses of *Fundulus heteroclitus*." *Biol. Bull. Wood's Hole*, **77**, 258–67.

BUTCHER, E. O. & ADELMANN, H. B. (1937). "The effects of covering and rotating the eyes on the melanophoric responses in *Fundulus heteroclitus*." *Bull. Mt Desert Id. Biol. Lab.* pp. 16–18.

CUNNINGHAM, J. T. (1893). "The problem of variation." *Nat. Sci.* **3**, 282–87.

—— (1895). "Additional evidence on the influence of light in producing pigments on the lower sides of flat fishes." *J. Mar. biol. Ass. U.K.* **4**, 53–9.

CUNNINGHAM, J. T. & MACMUNN, C. A. (1893). "On the coloration of the skins of fishes, especially of Pleuronectidae." *Philos. Trans.* (B), **184**, 765–812.

FISCHEL, A. (1920). "Beiträge zur Biologie der Pigmentzelle." *Anat. Hefte*, **58** (Heft 174), 1–136.

FLEMMING, W. (1882). *Kernsubstanz, Kern und Zelltheilung.* Leipzig.

—— (1897). "Ueber den Einfluss des Lichts auf die Pigmentierung der Salamanderlarve." *Arch. EntwMech. Org.* **48**, 369–74.

FRANZ, V. (1910). "Zur Physiologie und Pathologie der Chromatophoren." *Biol. Zbl.* **30**, 150–8.

v. FRISCH, K. (1911). "Beiträge zur Physiologie der Pigmentzellen in der Fischhaut." *Pflüg. Arch. ges. Physiol.* **138**, 319–87.

—— (1920). "Ueber den Einfluss der Bodenfarbe auf die Fleckenzeichnung des Feuersalamanders." *Biol. Zbl.* **40**, 390–414.

FUCHS, R. F. (1914). "Der Farbenwechsel und die chromatische Hautfunktion der Tiere." In Winterstein's *Handbuch der vergleichenden Physiologie*, Jena, 3 Bd., 1 Hälfte, 11 Teil, S. 1189–1656.

GIERSBERG, H. (1930). "Der Farbwechsel der Fische." *Z. vergl. Physiol.* **13**, 258–79.
—— (1932). "Der Einfluss der Hypophyse auf die farbigen Chromatophoren der Elritze." *Z. vergl. Physiol.* **18**, 369–77.
—— (1934). "Physiologie des Farbenwechsels bei Tieren." *Zool. Anz.* Suppl.-Bd. **7** (*Verh. d. deutsch. zool. Gesellsch.*), 96–126.
HERBST, C. (1919). *Beiträge zur Entwicklungsphysiologie der Färbung und Zeichnung der Tiere.* 1. *Der Einfluss gelber, weisser und schwarzer Umgebung auf die Zeichnung von* Salamandra maculosa. 64 pp. Heidelberg.
—— (1924). "Beiträge zur Entwicklungsphysiologie der Färbung und Zeichnung der Tiere. 2. Die Weiterzucht der Tiere in gelber und schwarzer Umgebung." *Arch. mikr. Anat.* **102**, 130–67.
HERBST, C. & ASCHER, F. (1927). "Beiträge zur Entwicklungsphysiologie der Färbung und Zeichnung der Tiere. 3. Der Einfluss der Beleuchtung von unten auf das Farbkleid des Feuersalamanders." *Roux Arch. EntwMech. Organ.* **112**, 1–59.
HEWER, H. R. (1927). "Studies in colour changes of fish. Part II. An analysis of the colour patterns of the dab. Part III. The action of nicotin and adrenalin in the dab. Part IV. The action of caffeine in the dab, and a theory of the control of colour changes in fish." *Philos. Trans.* B, **215**, 177–200.
—— (1931). "Studies in colour changes of fish. Part V. The colour-patterns in certain flatfish and their relation to the environment." *J. linn. Soc.* (Zool.), **37**, 493–512.
HIMMER, A. (1923). "Untersuchungen über den physiologischen und morphologischen Farbwechsel bei Amphibien." *Arch. mikr. Anat.* **100**, 110–63.
HOGBEN, L. T. (1924). *The Pigmentary Effector System.* 152 pp. Edinburgh and London.
—— (1936). "The pigmentary effector system. VII. The chromatic function in elasmobranch fishes." *Proc. roy. Soc.* B, **120**, 142–158.
HOGBEN, L. T. & SLOME, D. (1936). "The pigmentary effector system. VIII. The dual receptive mechanism of the amphibian background response." *Proc. roy. Soc.* **120**, 158–72.
KAMMERER, P. (1913). "Vererbung erzwungener Farbveränderungen. IV. Mitteilung. Das Farbkleid des Feuersalamanders (*Salamandra maculosa* Laurenti) in seiner Abhängigkeit von der Umwelt." *Arch. EntwMech. Org.* **36**, 4–193.
KEEBLE, F. & GAMBLE, F. W. (1904). "The colour-physiology of higher crustacea." *Philos. Trans.* B, **196**, 295–388.
KUDÔ, T. (1922). "Veränderung der Melaninmenge beim Farbwechsel der Fische *Esox*, *Carassius*, *Phoxinus*, *Gobius*, *Nemachilus*." *Arch. EntwMech. Org.* **50**, 309–25.
KUNTZ, A. (1917). "The histological basis of adaptive shades and colours in the flounder *Paralichthys albiguttus*." *Bull. U.S. Bur. Fish.* **35**, 1–29.
KURZ, F. (1920). "Versuche über den Einfluss farbigen Lichtes auf die Entwicklung und Veränderung der Pigmente bei den Fischen." *Zool. Jb.* (Abt. für allgem. Zool.), **37**, 239–78.
MAST, S. O. (1916). "Changes in shade, colour, and pattern in fishes, and their bearing on the problems of adaptation and behaviour, with especial reference to the flounders *Paralichthys* and *Ancylopsetta*." *Bull. U.S. Bur. Fish.* **34**, 173–238.
MAYERHOFER, F. (1909). "Farbwechselversuche am Hechte (*Esox lucius* L.)." *Arch. EntwMech. Org.* **28**, 546–60.
MEYER, EVA (1931). "Versuche über den Farbwechsel von *Gobius* und *Pleuronectes*." *Zool. Jb.* (Abt. für allgem. Zool.), **49**, 231–70.
MURISIER, P. (1920, 1921). "Le pigment mélanique de la truite (*Salmo lacustris* L.)." *Rev. suisse Zool.* **28**, 45–97, 149–95, 243–99.
ODIORNE, J. M. (1933). "Degeneration of melanophores in *Fundulus*." *Proc. nat. Acad. Sci., Wash.*, **19**, 329–32.
—— (1936). "The degeneration of melanophores in *Fundulus*." *J. exp. Zool.* **74**, 7–39.
—— (1937). "Morphological colour changes in fishes." *J. exp. Zool.* **76**, 441–65.
OGNEFF, J. F. (1908). "Ueber die Veränderungen in den Chromatophoren bei Axolotlen und Goldfischen bei dauernder Lichtentbehrung und Hungern." *Anat. Anz.* **32**, 591–607.
PARKER, G. H. (1930). "Chromatophores." *Biol. Rev.* **5**, 59–90.
—— (1932). *Humoral Agents in Nervous Activity, with special reference to Chromatophores.* Cambridge.
—— (1934*a*). "Neurohumors as activating agents for fish melanophores." *Proc. Amer. phil. Soc.* **74**, 177–84.
—— (1934*b*). "Colour changes in the catfish *Ameiurus* in relation to neurohumors." *J. exp. Zool.* **69**, 199–233.
—— (1936). "The reactions of chromatophores as evidence for neurohumors." *Cold Spr. Harb. Symp. Quant. Biol.* **4**, 358–70.
—— (1938). "Melanophore responses in the young of *Mustelus canis*." *Proc. Amer. Acad. Arts Sci.* **72**, 269–82.

PARKER, G. H. & LANCHNER, A. J. (1922). "The responses of *Fundulus* to white, black and darkness." *Amer. J. Physiol.* **61**, 548–50.
PARKER, G. H. & PORTER, H. (1934). "The control of the dermal melanophores in elasmobranch fishes." *Biol. Bull. Wood's Hole*, **66**, 30–7.
PEARSON, J. F. W. (1930). "Changes in pigmentation exhibited by the fresh-water catfish, *Ameiurus melas*, in response to differences in illumination." *Ecology*, **11**, 703–12.
PIETTRE, M. (1911). "Sur les pigments mélaniques d'origine animal." *C.R. Acad. Sci., Paris*, **153**, 782–85.
POUCHET, G. (1876). "Des changements de coloration sous l'influence des nerfs." *J. Anat., Paris*, **12**, 1–90, 113–65.
SCHNURMANN, F. (1920). "Untersuchungen an Elritzen über Farbenwechsel und Lichtsinn der Fische." *Z. Biol.* **71**, 69–98.
ŠECÉROV, S. (1909). "Farbenwechselversuche an der Bartgrundel (*Nemachilus barbatula* L.)." *Arch. EntwMech. Org.* **28**, 629–60.
SMITH, P. E. (1916). "The effect of hypophysectomy in the early embryo upon growth and development of the frog." *Anat. Rec.* **11**, 57–64.
SUMNER, F. B. (1911). "The adjustment of flatfishes to various backgrounds: a study of adaptive colour change." *J. exp. Zool.* **10**, 409–505.
—— (1933). "The differing effects of different parts of the visual field upon the chromatophore responses of fishes." *Biol. Bull. Wood's Hole*, **65**, 266–82.
—— (1935). "Evidence for the protective value of changeable coloration in fishes." *Amer. Nat.* **69**, 245–66.
—— (1939*a*). "Quantitative effects of visual stimuli upon pigmentation." *Amer. Nat.* **73**, 219–34.
—— (1939*b*). "Human psychology and some things that fishes do." *Sci. Mon., N.Y.*, **49**, 245–55.
—— (1940). "Further experiments on the relations between optic stimuli and the increase or decrease of pigment in fishes." *J. exp. Zool.* **83**, 327–43.
SUMNER, F. B. & DOUDOROFF, P. (1937). "Some quantitative relations between visual stimuli and the production or destruction of melanin in fishes." *Proc. nat. Acad. Sci., Wash.*, **23**, 211–19.
—— —— (1938*a*). "Some effects of light intensity and shade of background upon the melanin content of *Gambusia*." *Proc. nat. Acad. Sci., Wash.*, **24**, 459–63. (The title of this paper was unfortunately worded, inasmuch as no effect of light intensity was shown.)
—— —— (1938*b*). "The effects of light and dark backgrounds upon the incidence of a seemingly infectious disease in fishes." *Proc. nat. Acad. Sci., Wash.*, **24**, 463–6.
SUMNER, F. B. & FOX, D. L. (1933). "A study of variations in the amount of yellow pigment (xanthophyll) in certain fishes, and of the possible effects upon this of coloured backgrounds." *J. exp. Zool.* **66**, 263–301.
—— —— (1935*a*). "Studies of carotenoid pigments in fishes. II. Investigations of the effects of coloured backgrounds and of ingested carotenoids on the xanthophyll content of *Girella nigricans*." *J. exp. Zool.* **71**, 101–23.
—— —— (1935*b*). "Studies of carotenoid pigments in fishes. III. The effects of ingested carotenoids upon the xanthophyll content of *Fundulus parvipinnis*." *Proc. nat Acad. Sci., Wash.*, **21**, 330–40.
SUMNER, F. B. & KEYS, A. B. (1929). "The effects of difference in the apparent source of illumination upon the shade assumed by a flatfish on a given background." *Physiol. Zool.* **2**, 495–504.
SUMNER, F. B. & WELLS, N. A. (1933). "The effects of optic stimuli upon the formation and destruction of melanin pigment in fishes." *J. exp. Zool.* **64**, 377–403.
VEIL, CATHERINE (1936). "Sur le mécanisme du changement de couleur chez les poissons." *J. Physiol. Path. gén.* **34**, 824–39.
VILTER, V. (1931*a*). "Modifications du système mélanique chez les Axolotls soumis à l'action de fonds blancs ou noirs." *C.R. Soc. Biol., Paris*, **108**, 774–77.
—— (1931*b*). "Origine des cellules mélanisées." *C.R. Soc. Biol., Paris*, **108**, 941–3.
—— (1935). "Le mélanoblaste dendritique des vertébrés et sa signification fonctionnelle." *Bull. Soc. Fr. Derm. Syph.* (Réunion dermatologique de Strasbourg, Juillet, 1935), pp. 1–48.
—— (1937). "Rapports entre les champs rétiniens et l'activité sympathique locale de la peau de l'axolotl." *C.R. Ass. Anat., Marseille*, pp. 1–14.
—— (1938). "Recherches sur le déterminisme physiologique du dessin mélanique de l'axolotl (*Amblystoma mexicanum*)." *Arch. Anat. Strasbourg*, **26**, 1–252.
WARING, H. (1936). "Colour change in the dogfish (*Scyllium canicula*)." *Proc. Lpool biol. Soc.* **49**, 17–64.
ZONDEK & KROHN (1932). *Klin. Wschr.* **11**, 405, 849, 1293 (cited by Waring, 1936).

ADDENDUM

Since the foregoing review was prepared, Osborn (1940, *Proc. nat. Acad. Sci. Wash.* **26**, 155–61) has reported the results of recent experiments in illuminating flounders from below. This procedure resulted in a considerable development of pigment upon the lower, normally white, surface of the body, both in normal and in blinded fishes. These results were obtained with well-grown specimens (11 to 17 inches). The effects were manifest within a few weeks. The fact that blinded fishes kept on white backgrounds lighted from above also developed "unmistakable amounts of ventral pigment" suggests, as Osborn remarks, that vision is not essential to this process. But I think it likewise suggests that in his experiments with normal fishes the development of ventral pigmentation was not necessarily a direct response of the skin to illumination.

Contribution No. 99

DISCOLORED SEA WATER

By W. E. Allen

(Scripps Institution of Oceanography of the University of California)

Although the ocean, or any of its subdivisions, is far from being uniform or constant in color that condition usually receives scant attention. It is only when an observer notices some unexpected richness, or quality, or kind of color that he shows special interest in what he calls "discoloration." Because discolorations are subject to the same kinds of modifications as familiar or expected colors they are no more uniform or constant in appearance than the latter. That is to say, they differ somewhat according to the intensity of light, angle of light rays, amount of shading by clouds, movement of the mass of water, depth of the water, position of the observer, density of the coloring materials, and so on.

Apparently, discolorations sufficiently prominent to be logged by a mariner or to attract particular attention from a casual observer are nearly all produced by small (perhaps mostly microscopic) particles suspended in sea water. Some of these, more or less "muddy" in appearance, may be nothing more than soil particles carried into the sea by windstorms or "run-off" floods from land. In fewer instances dust from volcanic explosions may contribute. At times these may help to make conditions favorable for an ensuing development of discoloration by microscopic plants. Judging from the comments of mariners, explorers, fisheries employees, scientific expeditions, and biological observers, it seems safe to say that the discolorations which receive definite notice are usually caused by microscopic plants.

Some shade, or tinge, of red is most often mentioned in comments on discoloration of sea water. Probably such comments can be found as far back as recorded history can carry us and it is probable that there has been no change in the causes of "red water" in historic time. At sea, two great groups of microscopic plants are likely to contribute the species responsible in any particular instance. These are the diatoms and the dinoflagellates, More rarely, other groups may take the lead in causing discoloration, and the color may not be red. All kinds are so small that from 2 to 500 individual cells could be enclosed in a drop of sea water without overcrowding. Such tiny specimens show very little color when examined singly. It is only when densely crowded that the sum total of color becomes observable.

For more than 20 years diatoms and dinoflagellates have been under investigation at the Scripps Institution of Oceanography, La Jolla (near San Diego), Calif. In that time discolorations have developed in several different years. In June 1924, discoloration was continuous for more than 2 weeks, beginning with reddish-brown and ending with dirty brown or grayish-brown as the population died off and turned to "stinking water." The duration of this discoloration was exceptional, probably because of mild weather and quiet seas. A dinoflagellate called *Prorocentrum micans* was most prominent.

In 1935 a yellowish discoloration was observed close inshore for 2 or 3 days in the height of the bathing season. Some people were afraid that some kind of contamination was present. The creature causing the trouble was so small that even a microscope of ordinary power was not sufficient for adequate study. It was not identified.

In 1938 a dinoflagellate called *Gonyaulax polyedra* became excessively abundant in the general region of San Diego, sports fishermen claiming it spoiled the fishing over a large area outside of San Diego. The "red water" caused by it was visible near La Jolla for more than a week although great intensity of discoloration was noticed for only 4 or 5 days. Inshore discolorations are always streaky, partly because of wave action and the influence of currents. Any little ripple or wavelet is likely to show a thin streak of yellow froth, yellow partly because of mixture with air to form the froth. *Procentrum* is especially notable for froth streaks even when the population is too thin to discolor the water mass noticeably. The 1938 *Gonyaulax* population showed fewer narrow streaks of froth and more streaks varying from a foot to several yards in width. In these streaks the color ranged from light brownish-red to the dark red of drying blood most of the time, but on one day a few long wide streaks were seen which approached the bright red color of fresh blood.

Concerning the origins of discolorations there has been much speculation but very little accumulation of evidence because the details of origin are already matters of past history by the time that the discoloration is seen. In 1916 floods out of San Diego Bay were followed in several days by a widespread brownish discoloration caused by excessive growth of diatoms. The 1938, 1939, and 1940 cruises of the Scripps Institution research ship revealed the presence of discolored water at some stations a hundred miles or more from shore. For them Director H. U. Sverdrup was able to show a relation to "upwelling water." The 1924 "red water" mentioned above had neither of these relationships. Such differences in observations and experiences lead naturally to the conclusion that discolorations due to inclusions of microscopic creatures in sea water may be final steps in series of processes considerably unlike in details.

Localities (even regions) differ widely in their tendencies to produce or exhibit plant discolorations. In Southern California seas intense discolorations are comparatively rare in contrast to the Red Sea where a microscopic "blue-green alga" called *Trichodesmium* appears with such remarkable frequency as to suggest the name "Red," and to the Gulf of California which has received the name (in Spanish) "Vermillion Sea" because of the frequency of appearance of "red water," caused most often by dinoflagellates. Some observers have reported that wide areas of the Arctic Ocean often become so deeply discolored with dense growths of diatoms that they deserve the designation "black water." Likewise voyagers in the Antarctic have found diatoms to be so abundant in some places that they discolor both water and ice floes over great distances. In the recent "Discovery Reports" the waters near south Georgia are especially mentioned for exhibitions of discoloration by diatoms although similar conditions are noticed in other Antarctic localities. The "Humboldt Current" off the Peruvian coast has been notable for decades because of the prominence of plant discolorations, mainly diatoms.

In most localities displays of discoloration by microscopic plants tend to be seasonal, some time in the spring in temperate and frigid climates, thus corresponding in periodicity with land plants. Gray's Harbor, Wash., marks one locality in which discoloration by diatoms along shore is annual, in late May. The Malabar Coast in India appears to be even more notable in respect to annual discoloration because of kinds of creatures involved and because of successive differences in colors. There a relationship to the southwest monsoons has been observed and discoloration may become pronounced in September or October according to weather conditions. Colors reported according to different organisms involved or according to conditions of development are "amber-brown," "red," "bluish-green," "yellowish-green," "yellowish-red," and "amber."

Specific mention of localities in which discoloration is extreme and periodic may appear to warrant a conclusion that other localities (or the sea as a whole) are barren. The records of the Scripps Institution suggest that such a view is untenable. Included in the 25,000 collections obtained since 1917 are series of surface catches from California to Australia, to Hawaii, to Alaska, and to Peru, which show that even in mid ocean a few diatoms and dinoflagellates can be caught at almost any time. Even if only one vigorous specimen to a cubic fathom is found it carries the possibility of increasing to thousands in surprisingly few days if the right growing conditions are met. But we have some thousands of catches from waters within 200 miles of shore which indicate that living specimens may occur to depths of 50 fathoms or lower and that the numbers rarely get below some hundreds to a cubic fathom. That is to say, almost all oceanic waters contain enough "seed" specimens of one kind or another to produce a crop of plants of discoloring density within a period of 2 to 4 weeks according to circumstances. A thin, or a moderate, population may exist for months or years before it finds the combination of light, temperature, food materials, and other conditions which will enable it to show discoloration.

In general, it may be said that if a discoloration of the sea extends to the horizon, or beyond, it is likely to depend on the presence of microscopic plants, although accompanying circumstances may suggest "dust storms" or dust from volcanic explosions as being responsible. More limited discolorations may be due to any of an indefinite variety of causes.

Reprinted from Hydrographic Bulletin No. 2662, September 11, 1940
U. S. Hydrographic Office, Washington, D. C.

Contribution No. 107

SAND MOVEMENTS NEAR THE BEACH IN RELATION TO TIDES AND WAVES

By EUGENE C. LAFOND

*Contribution from the Scripps Institution of Oceanography, New Series, No. 107.

Reprinted from
PROCEEDINGS OF THE SIXTH PACIFIC SCIENCE CONGRESS
1939

SAND MOVEMENTS NEAR THE BEACH IN RELATION TO TIDES AND WAVES

By Eugene C. LaFond

Studies of sand movements and beach erosion have been carried on at La Jolla for several years in order to determine, first, the main factors which control the removal and deposit of sand on and near the beach, and secondly, the magnitude of the changes which might be expected in this region under various conditions. The work has been carried on as a joint enterprise with Dr. Francis P. Shepard and with the assistance of the Works Progress Administration. The following preliminary report* deals only with the effect of tide and waves upon the sand movements near the beach.

Measurements of sand elevations were determined by soundings from the Scripps pier. To avoid sounding in the depressions near the pilings, a boom was devised which extended ten feet out from the pier, and soundings were taken halfway between pilings, which are spaced twenty feet apart. This makes each measurement 14 feet from any obstruction. The device is constructed so as to roll on the rail and deck of the pier. Soundings were taken every 20 feet for 900 feet off the coast, and from these the profile of the bottom was determined. These measurements at 45 equally spaced stations, comprising the profile, were repeated once a week for two years, twice a week for one year, and daily from October, 1937, to October, 1938. In addition, for one 28-hour period measurements were made every 40 minutes along the entire length of the pier.

Other data taken in conjunction with the soundings include the tide height and wave character. The former is obtained from records of the Coast and Geodetic Survey's permanent tide gauge at the end of the pier.

The wave character was recorded by an automatic device which utilizes a large drum that floats on the water. It is guided in a vertical plane by two suspended wires. As a swell moves toward shore the drum is forced upward on these wires to the crest and then rides down to the trough. This vertical motion is transferred through a set of reduction gears to a recording pen. A cylinder revolving at a constant rate records the amplitude and frequency of the waves.

Relation to tides.—The effect of tidal cycles upon the sand movements was measured by W. F. Thompson[1] while conducting a study of the spawning of the grunion. He found that at Long Beach the sand on the upper part of the foreshore was deposited during an ebbing tide and cut away during a flooding tide. Similar observations have been made at La Jolla, from which it was concluded that, although such a sand movement usually occurs, its magnitude is so small that other factors may overshadow this tidal effect.

During a period of spring tides the profile of the beach was determined every 40 minutes for an interval of 28 hours. Changes in the beach profile were correlated not as much with the phase of the tide as with the amplitude of the waves. As the waves increased in size, the sand was moved in both directions away from the region near the plunge point; as the waves diminished in size, the sand moved back, reëstablishing the original profile.

---

*Contribution from the Scripps Institution of Oceanography, New Series, No. 107. Assistance in the preparation of these materials was supplied by the personnel of Works Progress Administration Official Project No. 665-07-3-141.

[1] Will F. Thompson and Julia Bell Thompson, "The Spawning of the Grunion," California State Fish and Game Commission, *Fish Bull. No. 3*, 29 pp., 1919.

The diurnal range of the tide, that is, the difference in height between the higher high water and lower low water during the day, is closely related to changes in the beach profile. The spring and neap tides have a semimonthly period which corresponds to a similar period in the sand elevation on the beach above and below mean sea level. It was found that the sand on the beach a few feet below mean sea level reached its greatest elevation two or three days after the greatest range in spring tides. Shortly after the minimum neap tide the sand at this position on the beach reached the lowest level. The sand elevation just above mean sea level shows a similar cycle but is out of phase with the sand height a few feet below mean sea level. From this it was concluded that the sand below mean sea level is eroded during neap tides to build up the beach near or above mean sea level. This is shown in figure 1, where the average sand elevations before and after neap tidal periods have been plotted for each quarter of the year. The first pair of curves, A, represents the averages observed in January, February, and March. Mean sea level is situated very near the nodal point of the sand shift. However, since the sand is cut and filled throughout the year, and as the quarterly mean sea

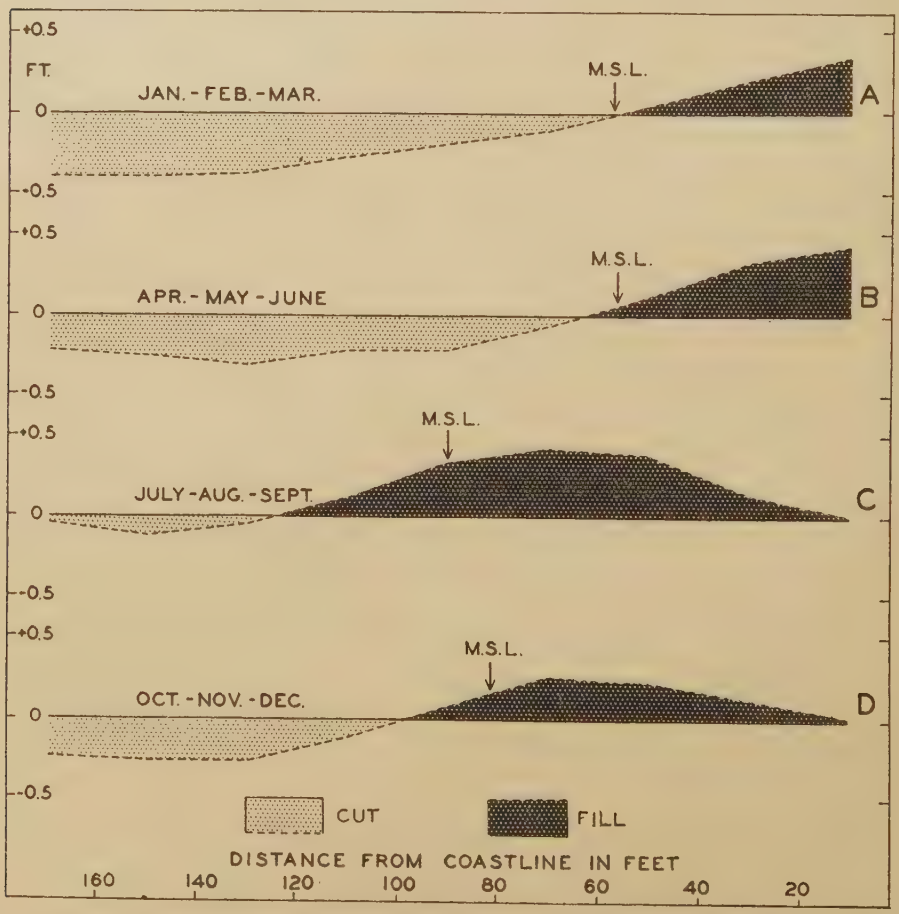


FIGURE 1. Average weekly change in sand elevation on the beach during neap tides for each quarter of the year and the relationship to the quarterly mean sea level (M. S. L.).

level also fluctuates, the distance from the coast line at which the mean sea level strikes the beach depends upon the season. From figure 1 it can be seen that the nodal point likewise moves simultaneously in the same direction as the mean sea level. During the last two quarters, C and D, the sand levels were higher and the high tides rarely covered the inner parts of the beach; consequently, little change occurred in this region. The average change in sand elevation during a series of neap tides is less than 0.5 foot at La Jolla.

Effect of waves.—The action of waves upon the beach is probably the strongest force effective in the movement of sand. Figure 2 is a tracing of wave records from three different days. These show the variability of waves recorded at La Jolla. The upper curve, A, is a record of waves having small amplitudes and short period; B, of waves of small amplitudes and long period; and C, of waves of large amplitudes. The time plotted along the abscissa is for six minutes. The height of the largest waves of A and B is about 2 feet, whereas that of C is 7 or 8 feet.

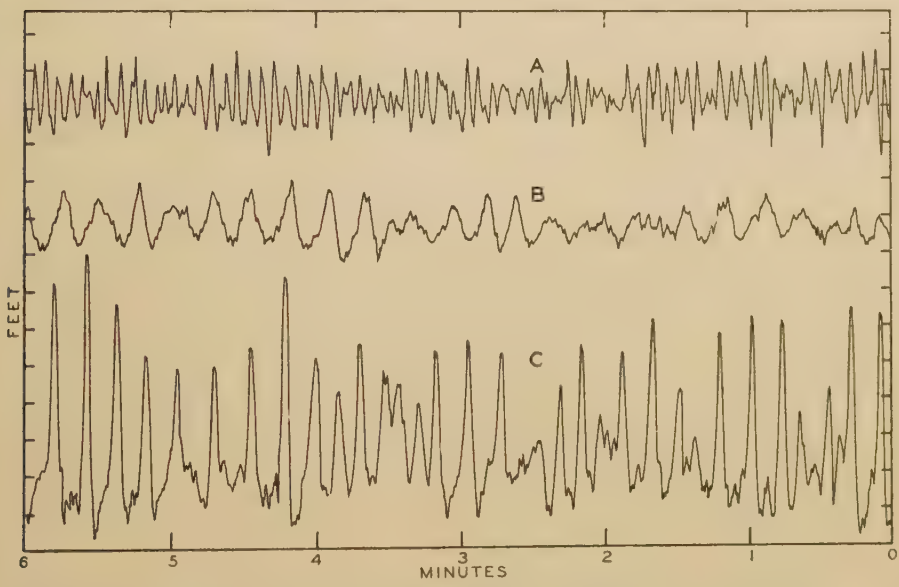


FIGURE 2. Three wave records illustrating the variability of waves received at La Jolla. A. Waves of low amplitude and short period. B. Waves of low amplitude and long period. C. Waves of high amplitude.

If we plot the period of the waves against their maximum height as observed during 5- to 15-minute intervals each day (figure 3, A), we find that the most frequent maximum height is between 2 and 4 feet. The solid line represents the frequency distribution for the various groups of wave periods. It can be seen that the most frequent wave period lies between 8 and 10 seconds. The large waves have a period near or slightly above the average; for the smaller waves a great range of periods was found.

To show the effect of waves of large and small amplitude, and of long and short period, upon the beach profile, 8 sets of observations for each of these conditions were chosen, and the average sand elevations before and after these times are plotted on figure 3, B, C, D, and E. The average of several sets of

observations was used to minimize the other factors which influence sand movements as well as give the changes which may be expected under these conditions.

It was also necessary to choose different intervals of time in order to compare the effect of the various wave forms upon the beach profile, since the action of some wave forms is much more pronounced than that of others.

The upper curves (fig. 3, B) represent the average changes which take place in the profile of the bottom during the first 24 hours of high waves. Subsequent days of high waves show less change, because of the increased depth of water. It can be seen that a continuous cut occurs between the highest point on the beach and a point about 10 feet below mean sea level. Below this level and out to at least 900 feet from the coast line there is an accumulation of sand. The average cut in 24 hours in the region near the plunge point, caused by waves with a maximum height ranging between 7 and 12 feet, is about 1.5 feet. In extreme cases 3.0 feet of sand have been eroded in this region. The erosion near the plunge point and the accumulation of sand on the seaward side is such that a depression or trough is formed. The fill beyond the trough is usually less than the amount removed from the inner part of the beach, owing to the transport of material beyond the range of these observations.

The second pair of curves (fig. 3, C) shows the average change in the profile which occurred during 3 days of long-period waves with an average maximum height of 3.0 feet and a period greater than 11 seconds. The resultant changes in the profile are similar to those caused by large waves, except that their magnitude is smaller.

The third pair of curves (fig. 3, D) represents the average change during 3-day intervals when the waves had the same average maximum height of 3.0 feet but were of short period, about 6 seconds. Under these conditions the change is small. However, in contrast to the long-period waves there is in general a slight fill over most of the section.

The last curves (fig. 3, E) illustrate the average change in the profile during intervals when there were 7 consecutive days of low waves. In the 8 weeks chosen the average maximum height of the waves was less than 2.5 feet. The resulting change is opposite in character to that of high or long-period waves, and evidence of a shoreward creep is shown by the increase of sand in the inner parts of the section at the expense of the outer parts. The weekly change in profile caused by low waves is much less than the effect of one day of very large waves. Nevertheless, these small waves are extremely important in building up the beach.

It should be remembered that these observations were made within a limited area and the extent to which these findings hold is uncertain. However, it was found that at La Jolla the sand movements are related to the tidal cycles and to the character of the waves, that is: (1) the sand elevation near or a few feet above mean sea level is usually increased during neap tides and decreased during spring tides; (2) the sand elevation a few feet below mean sea level is usually decreased during neap tides and increased during spring tides; (3) during waves of large amplitude and waves of long period the sand on the beach is cut away and redeposited in deeper water, and (4) during waves of short period and waves of small amplitude the sand elevation on the beach increases while the sand height decreases in the deeper water adjacent to the beach.

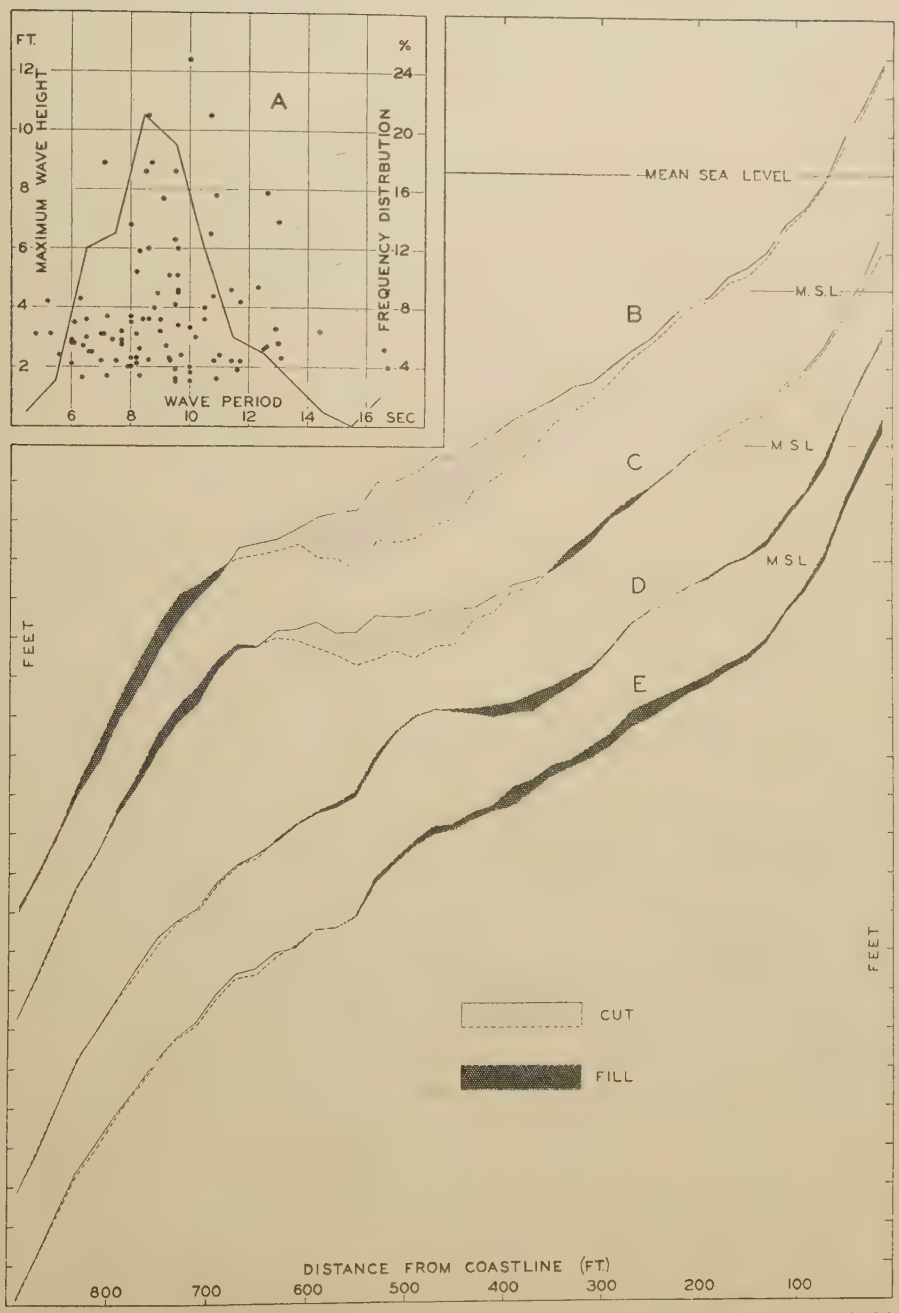


FIGURE 3. The relationship between the maximum wave height and the wave period is shown in A. The average change in the bottom profile is shown, in B, during the first day of very high waves; in C, during three days of long-period waves; in D, during three days of short-period waves; and in E, during one week of low-amplitude waves.

Contribution No. 111

Contributions from the Scripps
Institution of Oceanography
New Series, No. 111
(*Reprinted from* NATURE, *Vol.* 146, *page* 431, *September* 28, 1940.)

Submarine Geology and Geophysics

THE brief article by Dr. Bullard entitled "Geophysical Study of Submarine Geology" which appeared in NATURE of May 18, p. 764, was gratifying in that it directed attention to some of the developments in the newest field of geological research. On the other hand, this article showed a pardonable lack of familiarity with many developments, particularly with work along the California coast carried on with the facilities of the Scripps Institution. Since the tentative conclusions suggested by Dr. Bullard are in no way confirmed by these investigations, a brief summary of the work and its implications might prove of interest to the readers of NATURE. To date only brief summaries of this work have been published, but forthcoming publications by the Geological Society of America can be consulted for amplification.

Dr. Bullard referred to the excellent charts which have been prepared by the U.S. Coast and Geodetic Survey showing the submarine canyons which cut the submarine slopes off the American coasts. These charts have been used as a basis for oceanographic investigation of the submarine canyons on the auxiliary ketch *Atlantis* off the east coast and on the auxiliary schooner *E. W. Scripps* off the California coast. Since 1933, I have devoted a large amount of time to making minutely accurate charts of the canyon heads off California and in collecting samples of sediment and rock from the canyons and vicinity. Also accurate range lines have been established and checked many times to look for changing depths within the canyons. During 1938 approximately six months of cruises on the *E. W. Scripps* were devoted to this work.

The *E. W. Scripps* is equipped with a gravity coring device designed by K. O. Emery and R. S. Dietz, which obtains cores up to 10 ft. in length, equalling those obtained by the Piggot gun, which, contrary to the impression given by Dr. Bullard, has not obtained 10-ft. cores in rock but in oceanic ooze. Hundreds of cores have been obtained with this gravity device. Hundreds of dredgings of rock also have been taken with large geological dredges. Currents have been measured in a score of different places on the ocean bottom both in and out of submarine canyons. The echo-sounding device on the *E. W. Scripps* has also been employed particularly to find out about the nature of the outer termination of the canyons off southern California. Parallel

investigations of the east coast canyons have been undertaken by H. C. Stetson on the *Atlantis*.

Dr. Bullard states that the hypothesis that the submarine canyons are due to river cutting must be abandoned because the canyons extend to too great depths. However, it should be remembered that sea shells are found at high elevations in most mountain ranges. Before abandoning the river erosion hypothesis, would it not be better to look at some of the evidence from the canyon investigations? This evidence will, I think, prove disconcerting to those who wish to rule out the subaerial cutting. Thus we have found well-rounded gravel in cores and dredgings along the axis of many of the canyons and extending out to depths of so much as 5,000 ft. In places this gravel is mixed with shells which are certainly not of a deep-water variety. We have also found the water-worn gravel and even rounded cobbles on the banks off the California coast out to depths of 3,000 ft. At the head of the great Monterey submarine valley the deep fill shown by well cores gives unmistakable evidence of submergence great enough to account for at least a thousand feet of the submergence implied by the canyons.

The detailed surveys of the California submarine canyons reveal their close resemblance to the river canyons of the adjacent lands. These canyons are cut for the most part in rock. They have V-shaped cross-sections, winding courses, a river-like pattern of tributaries, and as continuous an outward slope as is typical of river canyons. While submarine processes are undoubtedly important in preventing the canyons from becoming filled, as is shown, for example, by the finding of submarine landslides, no process either of landslides or of submarine currents has as yet been detected which would appear to account for the canyon characteristics as well as that of subaerial origin. Our investigations show that the currents are not concentrated in the canyons nor do they attain proportions which could be expected to produce these great sea-floor gashes in the relatively short periods available for their excavation through the late Tertiary rocks found on their walls. These investigations cannot be said to have completely solved the mystery of the canyons, but they should at least show that one should not lightly dismiss the idea of subaerial excavation as has Dr. Bullard and as have various American writers in recent articles.

Dr. Bullard refers to the continental shelf as a mass of sediments built out on a gently sloping surface of rock. Possibly this interpretation may apply to some continental shelves, but again the evidence is largely in the opposite direction. Most

of the dredging operations both on the outer portion of the continental shelf and on the walls of submarine canyons which cut into the shelf margin have revealed the presence of rock. This is not only true off the California coast, where the evidence is incontrovertible, but also is the case off the New England coast where Stetson found well-consolidated Cretaceous rock at a depth of a few hundred fathoms near the shelf edge. When Dr. Bullard refers to the 8,000 ft. of sediments overlying the rock on the continental shelves off both sides of the Atlantic, he should qualify the statement by noting that it is not easy to distinguish between soft sedimentary rock and recent sediments in geophysical determinations. Also Ewing's work off eastern United States is only thought by that writer to imply a thick section of sediments and sedimentary rocks overlying the granite basement.

The statement that the edge of the shelf does not represent a fault scarp but is simply the outer edge of the sediment pile is also one that is subject to debate. The continental slopes show a close topographical resemblance to the fault scarps of the lands. Judging from deltas, they are distinctly too steep for normal sedimentary accumulations. The finding of rock in many places on the slopes is also significant in this connexion. Their straightness further implies fault origin. The deep water at the base of these slopes, despite the evidence that sediments are accumulating much faster at the slope base than on the slopes, indicates that diastrophism must be keeping the base depressed. Finally, the common presence of troughs in the ocean floor adjacent to the continental slopes and the seismicity of these zones lend support to the idea that the continental slopes are tectonic. Here again, however, it is best to reserve judgment until more evidence is available. Submarine geology is still too much in its infancy to make positive statements advisable.

FRANCIS P. SHEPARD.

Scripps Institution and
University of Illinois.
August 13.

PRINTED IN GREAT BRITAIN BY FISHER, KNIGHT AND CO., LTD., ST. ALBANS

Contribution No. 112

Reprinted from The Journal of Biological Chemistry
Vol. 136, No. 1, October, 1940

SOME FEATURES OF THE METABOLISM OF THE CAROTENOID PIGMENTS IN THE CALIFORNIA SEA MUSSEL (MYTILUS CALIFORNIANUS)*

By BRADLEY T. SCHEER

(From the Scripps Institution of Oceanography of the University of California, La Jolla, California)

(Received for publication, June 17, 1940)

One of the most striking features of marine organisms is the variety and intensity of pigmentation to be observed in many forms. Where the color is due to the presence in the tissues of chemical compounds, the possibility arises that the structure of such compounds makes them useful in the economy of the organism. The tissues of *Mytilus californianus*, where the underlying color is not masked by melanin, vary in color from very pale yellow to deep brick-red, depending on the condition of the animal, its sex, and other factors as yet undetermined. The structure of the animal is such that the pigmented tissues are not ordinarily exposed to light; it is then evident that the color, as such, can have no biological rôle, and that any importance which may be attached to the pigmentation of the tissues must perforce be physiological in nature.

Palmer (1922) was inclined to the view-point that carotenoid pigments were functionless, in the vertebrates at least; the subsequent discovery of the chemical nature of vitamin A, however, to a large extent invalidated Palmer's argument. The question now

* Contributions from the Scripps Institution of Oceanography, new series, No. 112.

This paper represents a portion of a thesis submitted to the Graduate Division of the University of California in partial satisfaction of the requirements for the degree of Doctor of Philosophy. The author wishes to express his indebtedness to Dr. D. L. Fox for his advice and assistance, to Mr. J. P. Cunningham and Mr. W. Thompson, of Federal Works Project No. 9964-D, and to Marlin Ann Ray Scheer, for technical assistance, and to Dr. G. Mackinney for samples of crystalline carotenoids.

remains, whether carotenoids other than vitamin A and its precursors have any function in animals. The discovery that invertebrate animals are able to synthesize specific animal carotenoids (Lederer, 1938) lends credence to the view that, among certain groups of invertebrates at least, colored carotenoids are important in metabolic processes. The only metabolic studies of the carotenoids of invertebrates known to the writer have been concerned with the zoosynthesis of pigments by Crustacea (Verne, 1926; Abeloos and Fischer, 1926; Fischer 1927; Teissier, 1932; Lwoff, 1927). The synthesis of carotenoids from colorless precursors by animals has not yet been demonstrated conclusively, although the paper of Lwoff gives strong evidence for the occurrence of such a synthesis.

Mytilus was selected for a metabolic study of carotenoids from the many pigmented organisms available because earlier studies from this laboratory (Fox *et al.*, 1936, 1937) had shown its suitability for physiological work and given some information regarding its physiology. This investigation aimed to secure information with respect to the nature, origin, and metabolism of the pigments of *Mytilus*.

Methods

Preparation of Animals—The animals used were all collected from the inshore pilings of the Scripps Institution pier. The mussels were detached at low tide, care being used to avoid tearing the byssus fibers, the adhering organisms were scraped off the shells, and the mussels placed in aquaria supplied with running sea water. They were left there for at least 12 hours to permit evacuation of fecal material. For studies of the effects of fasting and of feeding various diets, five to ten animals were placed in each of a number of glass jars of about 10 liters capacity, and sea water was added; the jars were then placed in a dark room kept at a constant temperature of 20°, and the water continuously aerated by a stream of fine air bubbles. The water was changed at appropriate intervals; distilled water was added when necessary to replace loss by evaporation.

Extraction and Separation of Pigments—The volume of the entire animal (shell volume) was first determined by displacement. The

mussel was then opened by severing the posterior adductor muscle; if a quantitative estimation of pigments was desired, the animal was inverted and the water drained out of the shell. The tissues were then dissected out, weighed, and extracted by grinding with sand under acetone. The extract was concentrated by evaporation under a stream of illuminating gas at temperatures ranging from 40–60°. The pigment was now passed into petroleum ether by dilution of the acetone with water; xanthophylls were separated from esters and carotenes by partition between petroleum ether and 90 per cent methanol. The details of these procedures are discussed by Zechmeister (1934), Lederer (1938), and Strain (1938).

The total amounts of hypophasic (xanthophylls) and epiphasic (carotenes and xanthophyll esters) pigment were now estimated by spectrophotometric measurements of the absorption of light of wave-length 485 mμ by a carbon disulfide solution of the pigments. This wave-length was chosen because it was found that the region of maximum absorption of mixtures of mussel pigments always lay between 480 and 490 mμ (see Figs. 1 and 4). The values obtained by such a measurement can only be expected to be proportional to the total concentration when the relative quantities of different pigments in the mixture remain the same; however, all of the pigments obtained from the mussel were found to have absorption maxima between 475 and 500 mμ, and the absorption at 485 mμ was in no case less than 90 per cent of that at the maximum (Fig. 2). The relative values obtained for concentration of total pigment should therefore be fairly accurate. For measurements, an aliquot portion of the solution containing all of either the hypophasic or epiphasic pigments was evaporated to dryness, and the pigment residue dissolved in 5 ml. of carbon disulfide (reagent grade). The measurements were made with a Bausch and Lomb visual spectrophotometer, reading directly in density, where this quantity is defined as $d = \log_{10} I_0/I$, d being the density, and I_0 and I being the intensity of a light beam after passing through equal and measured depths of pure solvent and pigment solution respectively. In solutions which follow Beer's law, $d = ecl$, where l is the length of the absorbing path in cm., c the molar concentration of the solution, and e a constant for any particular wave-length, known as the molecular extinction

(absorption) coefficient. The measurement of density then affords a measure of the concentration if the extinction coefficient is known. The extinction coefficient of individual pigments was determined by measuring the density of solutions containing known concentrations of purified pigment. For mixtures, the extinction coefficient of crystalline β-carotene at 485 mμ was arbitrarily selected as a standard.

Individual pigments were separated by the chromatographic adsorption method of Tswett (Zechmeister and von Cholnoky, 1937). Calcium carbonate (precipitated chalk, U.S.P.) was generally used as an adsorbent, it having been found to give the best separation of mussel pigments. As solvent, petroleum ether, benzene, or ethylene dichloride was used; in most routine analyses, benzene proved most satisfactory. For elution, a mixture of 1 part of absolute ethanol with 99 parts of petroleum ether was usually successful.

Total lipids were determined by extracting the dried tissues with petroleum ether in a Soxhlet apparatus. The total lipid extract was saponified, and the organic acids separated from the non-saponifiable matter by partition between basic alcohol and ethyl ether. Organic nitrogen was determined by the Kjeldahl method on the fat-extracted tissues.

Carotenoid Pigments of the Mussel

Hypophasic Pigments—When the carbon disulfide solution of the mixed hypophasic pigments of the mussel is examined with the spectrophotometer, absorption curves similar to those shown in Fig. 1 are found. The curves shown represent most of the types obtained. It was concluded from studies of these curves that the pigments of the mussel are the same qualitatively in the two sexes, at any season, and after prolonged fasting. This conclusion is fully borne out by a study of the chromatograms obtained by passing benzene solutions of the pigments through columns of calcium carbonate. Minor differences in position and relative quantities of various pigments are seen, but, on the whole, the composition of the chromatograms is sufficiently uniform to justify the description of a typical chromatogram.

Least strongly adsorbed, and hence near the bottom of the column, is a broad yellow band (Pigment I, Fig. 2). This pigment

has been crystallized, but in too small quantities to permit of a study of all of its properties. Its spectrum, with maxima at 460,

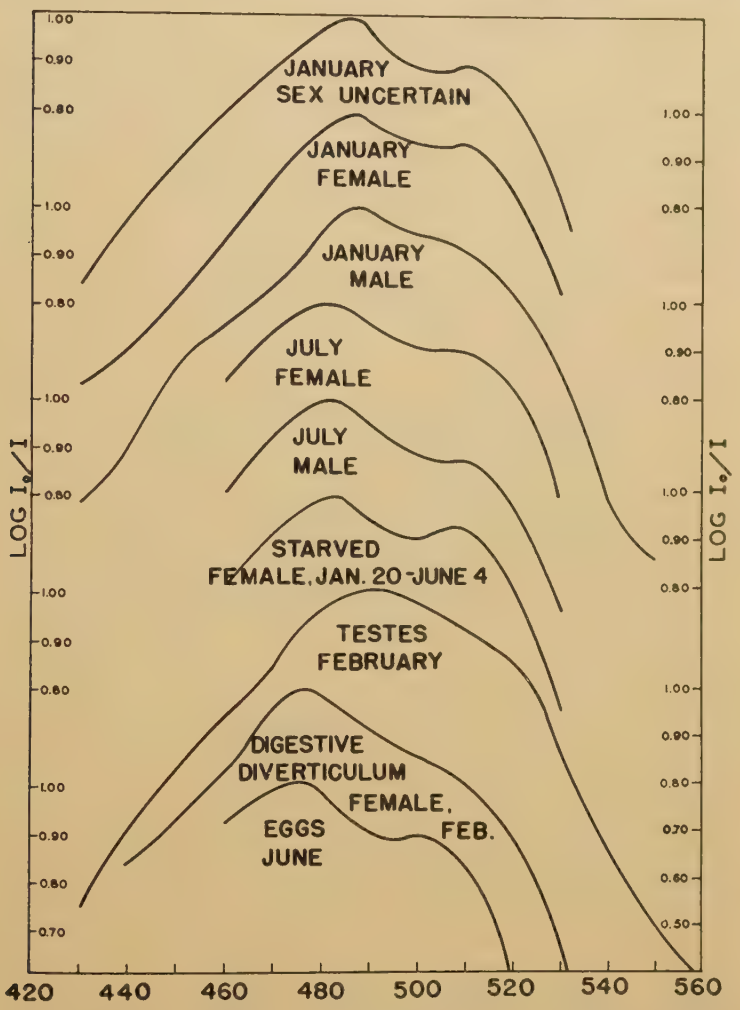


FIG. 1. Absorption spectra of hypophasic extracts of *Mytilus* tissues in carbon disulfide. Abscissae, wave-lengths in mμ; ordinates, density ($\log_{10} I_0/I$). The curves were determined by adjusting the depth of the solution so that the observed density at the maximum was equal to 1.00 (ratio of transmitted to absorbed light = $I_0/I = 10$). The ordinates on the left and right sides, respectively, refer to alternate curves.

482, and 513 mμ,[1] resembles those of several xanthophylls; by use of the "three tube test" (Lederer, 1938) it was proved to be identical with zeaxanthin, secured from Dr. H. Strain's laboratory through the kindness of Dr. G. Mackinney.

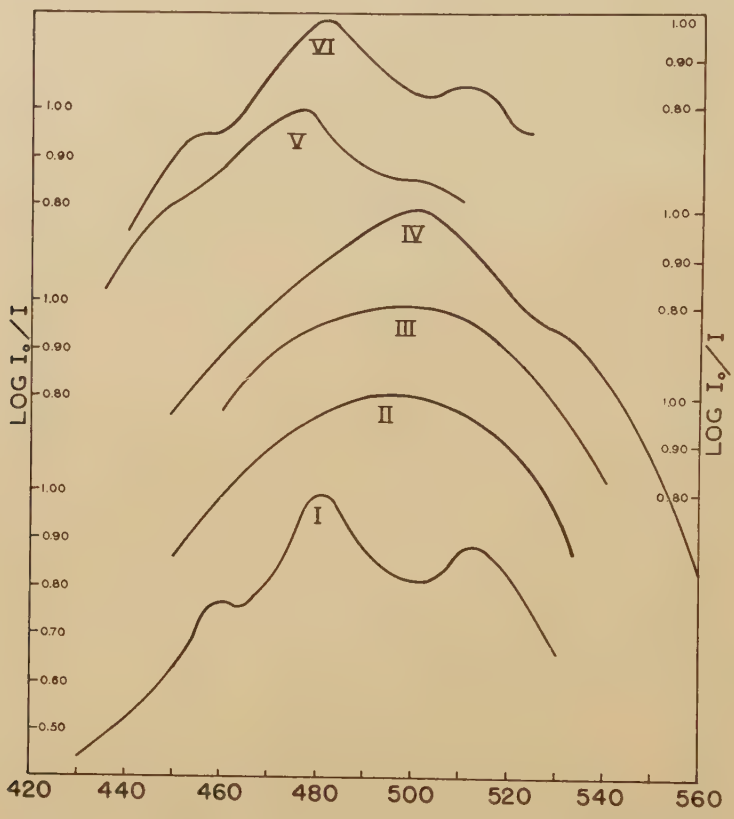


FIG. 2. Absorption spectra of individual hypophasic pigments (represented by roman numerals) from *Mytilus*. Abscissae, wave-lengths in mμ.

Above Pigment I, there always appears a thin red band (Pigment II). This pigment has not been crystallized. It lacks acidic properties, as does the similar pigment called glycymerin by Fabre

[1] Smith (1936) has studied the effect of the use of different instruments in measuring absorption spectra of carotenoids. The experimental values reported here were obtained with the visual spectrophotometer. Others are those cited by Strain (1938).

and Lederer (1934). The absorption curve of glycymerin is less symmetrical than that of Pigment II, however. Above Pigment II, there sometimes appears a thin red band (Pigment III) which is suspected of being a decomposition product of Pigment IV.

Pigment IV is present as a very broad red band, sharp below and fading to pink above. It has been obtained in crystalline state. Several hundred mussels were ground in a meat grinder and extracted with acetone. The acetone extracts were concentrated by boiling, and the pigment then taken up in petroleum ether. The hypophasic material was extracted with 90 per cent methanol, and then forced into petroleum ether by dilution with water. Some pigment separated as a flocculent precipitate at this point. The precipitate was dissolved in benzene. The petroleum ether solution was dried and evaporated, the residue likewise being dissolved in benzene. Both solutions were chromatographed. Pig-

FIG. 3. Crystals of mytiloxanthin, from methanol-water. × 400

ment IV was separated from the other pigments, eluted, and dissolved in benzene. Addition of petroleum ether caused formation of an amorphous solid mass of pigment. This was filtered out and dissolved in methanol. Addition of water resulted in the formation of bundles of poorly defined rods (Fig. 3) decomposing at 128–131° (Berl block; corrected). Recrystallization from benzene-petroleum ether gave an amorphous precipitate decomposing at 140–144° (Berl block; corrected). Both samples were dried for several hours *in vacuo* at 60°.

The pigment is soluble in benzene, carbon disulfide, and methanol, but only slightly soluble in petroleum ether. It is hypophasic in the partition test between 80 per cent methanol and petroleum ether, but migrates into the petroleum ether layer when the methanol is diluted to 70 per cent. The addition of base to a solution of the pigment in alcohol causes an immediate change in

color from red to yellow. Acetic acid reverses this change. When base is added to a biphasic system consisting of 70 per cent methanol, petroleum ether, and Pigment IV, the pigment forms a scarlet-red precipitate at the interface. Addition of acetic acid to the point of neutrality causes the pigment to return to petroleum ether. The pigment is resistant to treatment with alkali; after $3\frac{1}{2}$ hours at 70° in 5 per cent KOH in methanol, chromatographic comparison gave no evidence of change in composition. This pigment will be referred to in this paper as mytiloxanthin, since its properties are different from those of any carotenoid previously described. It is interesting to note that this pigment occurs in the tissues as a free acid, in contrast to astacin, which is found in many tissues as the neutral astaxanthin (Kuhn and Sörensen, 1939). It should also be noted that frequent studies of the feces, which represent a fair sample of the ingested food in view of the inefficiency of the digestive tract of the mussel, have failed to show any evidence of the presence of mytiloxanthin in the food of the mussel. Mytiloxanthin was also found to be absent from the diatom *Nitzschia closterium*, which is a constituent of the food of the mussel.

Above mytiloxanthin may occur yellow and orange bands of the type represented by Pigments V and VI. There are also found here from time to time pigments with spectra like those of Pigments III and IV. It is possible that some of these pigments are decomposition products of the main components. Pigment V, however, has a spectrum like those described for pentaxanthin (444, 474, 506 mμ) and fucoxanthin (477, 510 mμ), pigments which might be expected to occupy a similar position on the chromatogram. Pigment VI may be one of the isomers of zeaxanthin described by Zechmeister, von Cholnoky, and Polgár (1939).

Epiphasic Pigments—In Fig. 4 are presented the absorption spectra of epiphasic extracts from the same animals and tissues as the hypophasic extracts of Fig. 1. It is evident that the epiphasic spectra are as uniform as those from the hypophasic extracts, with the single exception of the extracts of the digestive diverticulum. Here, chlorophyll derivatives and other substances with strong absorption in the violet region obscure the spectra of the carotenoids. The nature of these obscuring substances has not been investigated. The chromatogram of the epiphasic extracts on

calcium carbonate is remarkably similar to that of the hypophasic extracts. Substances identical in position on the chromatogram

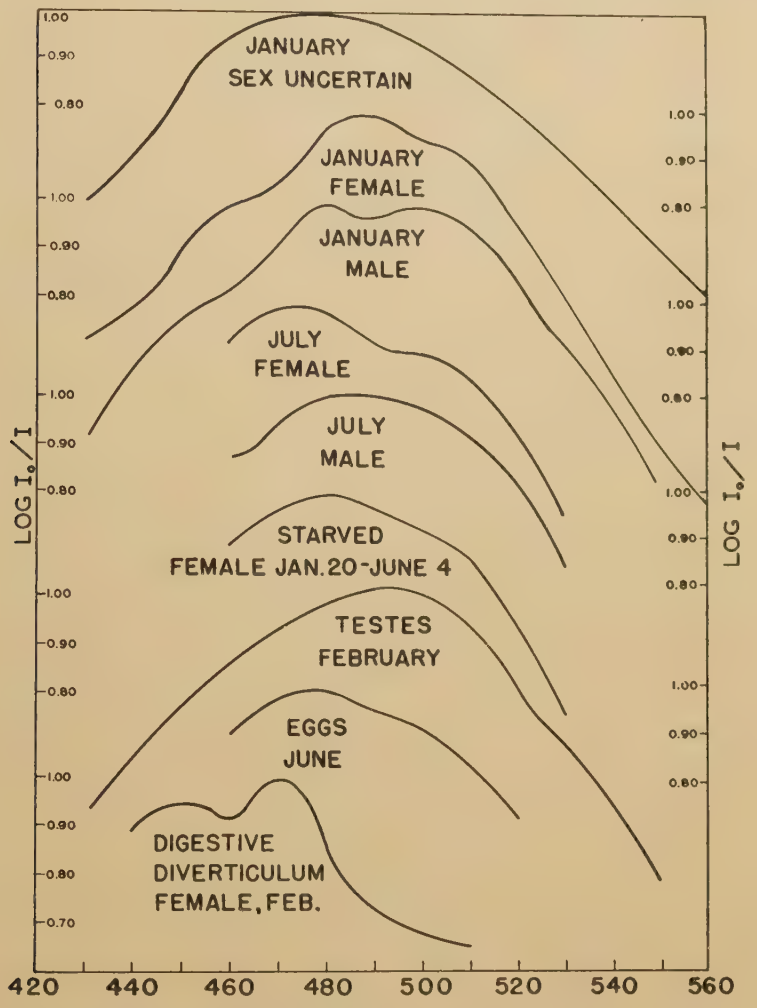


Fig. 4. Absorption spectra of epiphasic extracts of *Mytilus* tissues, in carbon disulfide. Abscissae, wave-lengths in mμ.

and in absorption spectra with Pigments I and IV have been observed; both become hypophasic after hydrolysis, and are prob-

ably esters of zeaxanthin and mytiloxanthin respectively. Two or three other bands, of small intensity and uncertain occurrence, appear from time to time. The remarkable fact, however, is that all of the pigments in the epiphasic fraction are strongly adsorbed to calcium carbonate. Very rarely, in mussels collected only a few hours before analysis, small quantities of pigments not adsorbed to calcium carbonate are observed; these are presumably carotenes. Otherwise, carotenes seem to be completely absent from the mussel, despite the fact that they are undoubtedly present in the plant material which serves as the principal food supply of this animal. Substances behaving like carotenes in respect to partition between solvents and adsorption affinities were observed in the diatom *Nitzschia closterium* and the dinoflagellate *Prorocentrum micans*, both of which (Buley, in Fox *et al.*, 1936) serve as food for the mussel, and in the feces of animals fresh from the sea.

In June, 1939, advantage was taken of the presence in the sea water off the Institution pier of large numbers of *Prorocentrum* to secure further data regarding this question. Approximately 1.5 gm. of these organisms were collected by filtering the water through a fine silk net and by centrifuging. At the same time, a sample of mussels, which had presumably been feeding on these organisms, was collected and the feces obtained. The feces, judging from the amount of light absorbed by a carbon disulfide solution of the pigments at 485 mμ, contained 4.38 mg. per cent of hypophasic pigment, while the plankton contained only 2.26 mg. per cent. However, the feces contained 0.752 mg. per cent of epiphasic pigment, while the dinoflagellates contained only 0.258 mg. per cent. That is, the ratio of hypophasic to epiphasic pigment in *Prorocentrum* was about 9:1, while the same ratio for the mussel feces was 6:1, indicating definite selection of hypophasic material in the digestive tract of the mussel.

Effects of Fasting and of Certain Other Physiological Changes on Pigments of the Mussel

Seasonal and Sexual Variations—During the winter, spring, and summer of 1939, approximately 50 normal mussels were analyzed individually for carotenoid pigments. The range of concentrations of hypophasic pigments was from 1.00 to 9.60 mg. per cent. (It should be noted that the values for concentrations and weights

given in this section of the paper are only relative, being based on determinations of the light absorbed at 485 mμ, and expressed in terms of mg. of β-carotene.) The female mussels occupied the upper portion of the range (1.76 to 9.60 mg. per cent, mean 4.95 ± 0.421, standard deviation 1.93), while the males had in general smaller concentrations of pigment (1.00 to 6.45 mg. per cent, mean 2.21 ± 1.27, standard deviation 1.32). No striking seasonal variation was apparent, although the analysis of larger numbers throughout the year might have shown some slight changes. No correlation between size and carotenoid concentration could be established.

The epiphasic pigments did not show the same relation to sex. The range obtained for males was 0.182 to 0.72 mg. per cent, with a mean value of 0.356 ± 0.03 and a standard deviation of 0.147. The values for females covered virtually the same range, from 0.169 to 0.864 mg. per cent, mean 0.34 ± 0.04, standard deviation 0.174. Again there was little evidence for any variation with season of the year or size of the animal.

Effects of Fasting—Preliminary studies were carried out in which it was attempted to alter the concentration of carotenoid by prolonged fasting. The results were insufficient to show any definite trend, except that as much as 3 months of fasting did not appear to cause any significant reduction in either epiphasic or hypophasic pigments. A carotenoid-free diet, consisting of 1 part of finely ground casein, 3 parts of starch (arrowroot or corn-starch), and 0.01 part of cholesterol was fed to certain other mussels, being suspended in the water with the mussels, and replenished as fast as removed by them. The mussels ingested this food, as was evident from the presence of abundant white feces in the jars. However, no change in total weight occurred in approximately 2 months of such feedings, during which time a control group of mussels kept in the sea at the end of the pier nearly doubled in weight. Two mussels, fasted from January 20 to May 1 and from June 23 to August 2, and fed on this diet in the intervening period, contained respectively 0.446 and 0.591 mg. per cent of epiphasic, and 3.80 and 6.29 mg. per cent of hypophasic pigments. In view of the fact that the latter animal was a male, the former being of indeterminate sex, these results would indicate that in a total period of 196 days without carotenoids no appreciable change in concentration occurred.

To test these observations carefully was subsequently attempted. Approximately 200 mussels were collected on August 17, 1939. Of these 150 were distributed among fifteen jars of sea water in a dark room at a temperature of 20°. The other 50 were analyzed as rapidly as possible. Of the fifteen experimental jars, the mussels in eight remained without food; those in another three were fed on a basal diet consisting of 1 part of dried brewers' yeast, 2 parts of casein, and 7 parts of corn-starch. The food mixture was known to yield no pigment to any of the normal carotenoid solvents. The animals in the remaining three jars were fed a pure culture of *Nitzschia closterium*. The feedings were initiated after a month of preliminary fasting, and were continued during approximately 3 months. The basal diet was usually

TABLE I

Effect of Fasting and of Various Diets on Body Weight of Mussels, Expressed by Change in Ratio of Shell Volume to Tissue Weight

Treatment	Time	Shell volume (ml.) / Tissue weight (gm.)	Shell volume (ml.) / Soma weight (gm.)	Shell volume (ml.) / Gonad weight (gm.)
	days			
Fasting	0- 30	2.50 ± 0.04	4.33	6.93
"	43- 74	3.03 ± 0.07	4.94	9.38
"	116-124	3.49	5.50	10.20
"	146-175	4.00	5.95	14.85
Nitzschia	138-169	3.60	5.64	11.12
Basal	140-160	3.92	6.09	14.45

added to the jars as rapidly as it could be removed by the mussels. About 1 liter of relatively concentrated *Nitzschia* suspension was added to each of the three jars daily. Both diets were readily ingested. The water was changed weekly in all but the jars containing the animals on the basal diet, in which it was changed daily. Feedings were usually made on 5 days of each week.

Effect on Tissue Weight—As a measure of the effectiveness of the various experimental treatments, the ratio of shell volume to wet weight of tissues was selected. The average values of this ratio for various intervals and tissues are presented in Table I. The ratio of volume to total tissue weight appears to increase linearly at a rate of approximately 0.01 per day, over the period of the

experiment. If this weight loss is assumed to result solely from the combustion of carbohydrate, a value for the oxygen consumption of the mussel at 20° of 1.25 cc. of O_2 per gm. per hour is obtained. Whedon and Sommer (1938), measuring this quantity directly, obtained values ranging from 0.3 to 2.0 cc. *Nitzschia* feeding appears to retard this weight loss, but the basal diet is without effect.

Effects of Fasting, Etc., on Individual Tissues—In order to learn whether the observed sexual differences in pigmentation were due simply to the accumulation of pigment in the ova, and to follow the movement of pigment within the body during fasting, the gonads and somatic tissues were separated in most of the analyses. From the first, it was found that the differences in concentration of hypophasic pigment were not confined to the gonads, but

TABLE II

Mean Concentration (in Mg. Per Cent) of Pigments in Gonads and Somatic Tissues of Twenty Mussels, Collected August 17, 1939, and Analyzed before September 3, with Sexual Differences and Their Standard Errors

Sex	Hypophasic pigment		Epiphasic pigment	
	Soma	Gonad	Soma	Gonad
Male	1.90 ± 0.25	5.36 ± 0.59	0.285 ± 0.08	0.691 ± 0.08
Female	4.42 ± 0.19	10.97 ± 2.3	0.413 ± 0.06	0.370 ± 0.05
Difference	2.52 ± 0.31	5.61 ± 2.4	0.128 ± 0.10	−0.321 ± 0.09

extended as well to somatic tissues. This is shown in Table II. If we choose to consider as significant only those differences which are at least twice their standard errors, we find that the hypophasic pigments of both somatic and gonad tissues and the epiphasic pigment of the gonads differ significantly in concentration between male and female tissues. The concentration of hypophasic pigment can be considered to be a true secondary sex characteristic, while that of epiphasic pigment is apparently dependent only on the accumulation of pigment in the testes, the composition being relatively uniform in all other tissues.

The results of analyses of fasted animals, and of those fed on various diets, showed no significant changes in concentration of either type of pigment in either somatic or gonad tissue. This

relative constancy of pigment concentration suggests that the disappearance of pigment proceeds at the same rate as the loss of weight by the fasting animal. Table III indicates the rate of weight loss. It is immediately evident that the weight loss is sustained mainly by the gonads, that the basal diet has no effect in retarding this loss, but that feeding *Nitzschia* serves to retard it to some extent. It should be noted that the effect of *Nitzschia* is exerted chiefly on the gonads.

Changes in Absolute Quantity of Pigment—To determine the rate at which pigment disappears, the data in Table II were used to calculate the average initial amount of pigment in a typical mussel having a shell volume of 125 ml., with tissues weighing 50 gm. The average concentration of pigment at the conclusion of the various experimental treatments was then used to determine the amount of pigment remaining in a mussel of the same shell volume, with a tissue weight corresponding to the values in Table I. The resulting quantities are presented in Table III. It will be noted that in many instances only a few animals were available for analysis. The figures must consequently be regarded as indicative only of trends.

We observe an apparent increase in amount of pigment in the ovaries of two females surviving fasting for approximately 120 days. However, this increase does not constitute proof of synthesis, in view of the fact that certain normal females had amounts of pigment slightly greater than those attained by these two animals. A high degree of retention of pigment is indicated, however. The epiphasic pigments of the ovaries of fasted females appear to increase regularly in amount with time; those females fed with *Nitzschia* have a larger amount than did the normal females at the beginning of the experiment, but somewhat less than did the females at 65 days; those fed the basal diet show a definite but small decrease in amount. It should also be noted that the largest decreases recorded in Table III are those observed in animals fed the basal diet; the ovaries, testes, and female somatic tissues especially lose large quantities of hypophasic pigment, while the testes and the somatic tissues of both sexes lose epiphasic material. In the fasted animals, the testes show the greatest and most consistent loss of hypophasic and epiphasic pigments alike. Except for the fact that the feeding of *Nitzschia* appears to retard the

TABLE III

Changes in Concentration and Total Weight of Pigment during Fasting and on Feeding Various Diets

Concentrations and weights are expressed as equivalent to mg. of β-carotene.

		Females					Males				
		Fasting			*Nitzschia*	Basal diet	Fasting			*Nitzschia*	Basal diet
Time, *days*		10	65	120	150	150	10	65	150	150	150
No. of animals		7	5	2	1	3	12	5	4	4	1
Tissue weight, *gm.*	Soma	28.8	25.3	22.8	22.2	20.6	28.8	25.3	21.0	22.2	20.6
	Gonad	18.1	13.3	12.2	11.2	8.66	18.1	13.3	8.42	11.2	8.7
Concentration of hypophasic pigment, *mg.* %	Soma	4.42	4.33	4.26	3.96	2.09	1.91	0.86	1.47	1.49	0.68
	Gonad	10.5	12.5	29.0	14.9	7.21	5.36	4.45	5.23	7.92	2.38
Weight of hypophasic pigment, *mg.*	Soma	1.27	1.20	0.970	0.880	0.430	0.551	0.216	0.309	0.331	0.140
	Gonad	1.91	1.66	3.54	1.67	0.625	0.970	0.592	0.441	0.889	0.207
Concentration of epiphasic pigment, *mg.* %	Soma	0.413	0.554	0.398	0.416	0.252	0.294	0.220	0.230	0.242	0.142
	Gonad	0.393	0.828	1.86	0.828	0.668	0.699	0.659	0.881	0.810	0.592
Weight of epiphasic pigment, *mg.*	Soma	0.119	0.140	0.091	0.093	0.052	0.085	0.051	0.048	0.054	0.029
	Gonad	0.071	0.110	0.226	0.093	0.058	0.126	0.088	0.074	0.091	0.051

loss of pigment from the tissues of males, the other changes are not of great significance.

Changes in Individual Pigments—In addition to the analysis of total pigments, the changes in concentration of zeaxanthin and mytiloxanthin were also followed. These results are summarized in Table IV. It should be noted that the values for concentration and absolute weight are here exact, being based on measurements of the absorption coefficients of pure compounds, whereas the values for total pigments were only roughly proportional to actual concentrations and weights. There appears to be a definite increase in the concentration of zeaxanthin in all tissues of fasted mussels of both sexes. Moreover, there is a definite increase in the total amount of zeaxanthin present in all tissues of other animals as well, with the single exception of the gonads of the males fed the basal diet. This increase is largest in the ovaries of fasted females, and is especially evident in the gonads of those animals fed *Nitzschia*. Mytiloxanthin, on the other hand, appears to decrease slightly in concentration. There is evidently a decrease in the absolute amount of mytiloxanthin in all but the males fed *Nitzschia*; here there is a relatively large increase in the testes, and a smaller increase in the somatic tissues. The largest decreases are observed in the gonads of the animals fed the basal diet; the somatic tissues of such animals show a decrease, as do the females fed *Nitzschia*.

Effects of Spawning on Carotenoid Content—During the course of the experiment, spawning occurred in more than half of the jars. The only consistent feature of the spawning was that it invariably occurred from 1 to 12 hours after the water had been changed; none occurred during the first 2 months of the experiment, but spawning was observed at frequent and more or less regular intervals during the succeeding 3 months. It was not possible to observe which mussels in a given jar were spawning; it was therefore necessary to assume that all mussels in a jar in which spawning was observed had spawned.

Table V shows the weights of the tissues and the amounts of pigment present in these mussels, compared with the same quantities in unspawned mussels treated similarly. Unfortunately none of the animals fed *Nitzschia* spawned. The values are all computed in the same way as those in Tables III and IV from

TABLE IV

Changes in Concentration and Weight of Zeaxanthin and Mytiloxanthin during Fasting and on Various Diets

The weights are exact, being based on absorption coefficients of the pure compounds.

		Females				Males			
		Fasting		*Nitzschia*	Basal diet	Fasting		*Nitzschia*	Basal diet
Time, *days*		65	150	150	150	65	150	150	150
No. of animals		5	2	1	3	4	4	4	1
Tissue weight, *gm.*	Soma	25.3	21.0	22.2	20.6	25.3	21.0	22.2	20.6
	Gonad	13.3	8.42	11.2	8.66	13.3	8.42	11.2	8.66
Concentration of zeaxanthin, *mg.* %	Soma	0.527	1.32	0.818	0.979	0.075	0.348	0.541	0.116
	Gonad	1.35	8.65	4.44	3.22	0.631	1.67	3.25	0.497
Weight of zeaxanthin, *mg.*	Soma	0.133	0.278	0.182	0.202	0.019	0.044	0.120	0.024
	Gonad	0.180	0.728	0.497	0.278	0.084	0.141	0.364	0.043
Concentration of mytiloxanthin, *mg.* %	Soma	2.06	1.67	1.58	1.48	0.576	0.456	0.723	0.191
	Gonad	7.92	10.98	7.92	6.40	2.90	2.87	4.88	0.710
Weight of mytiloxanthin, *mg.*	Soma	0.521	0.351	0.352	0.305	0.146	0.096	0.160	0.039
	Gonad	1.05	0.925	0.889	0.545	0.386	0.241	0.548	0.062

observed tissue weights for the spawned animals. In general it may be said that the amounts of pigment are greater in normal than in spawned fasted animals, with the reverse being true of

TABLE V

Effect of Spawning on Amount of Carotenoid (in Mg.) in Mussels Fasted and Those Fed Basal Diet

	Tissue	Fasting	Spawned	Basal diet	Spawned
		Tissue weight, gm.			
	Soma Gonad	21.0 8.42	22.0 7.03	20.6 8.66	21.9 7.63
		Females. No. of animals			
		2	5	3	4
Epiphasic pigment	Soma	0.091	0.078	0.052	0.065
	Gonad	0.226	0.102	0.058	0.136
Hypophasic pigment	Soma	0.970	0.724	0.430	0.469
	Gonad	3.54	0.980	0.625	0.926
Zeaxanthin	Soma	0.278	0.210	0.202	0.141
	Gonad	0.728	0.287	0.278	0.274
Mytiloxanthin	Soma	0.351	0.319	0.305	0.176
	Gonad	0.925	0.438	0.545	0.505
		Males. No. of animals			
		4	2	1	2
Epiphasic pigment	Soma	0.048	0.036	0.029	0.042
	Gonad	0.074	0.044	0.051	0.069
Hypophasic pigment	Soma	0.309	0.246	0.140	0.164
	Gonad	0.441	0.504	0.207	0.352
Zeaxanthin	Soma	0.044	0.062	0.024	0.042
	Gonad	0.141	0.171	0.043	0.111
Mytiloxanthin	Soma	0.096	0.103	0.039	0.053
	Gonad	0.241	0.195	0.062	0.129

animals fed the basal diet. The results of both carotenoid content and tissue weight measurements for spawned animals fed the basal diet are contrary to those for normal animals in that both tissue weights and carotenoid contents are generally higher in the

spawned animals. Either the two groups were not comparable at the beginning of the experiment, or these particular animals were able to make use of the basal diet, both for tissue formation and for the synthesis of carotenoids.

Aside from these results, however, it can be said that in general the amount of carotenoids present in the gonads of fasted mussels decreases subsequent to spawning. This would be expected in females, for which analysis of shed ova shows the following composition: epiphasic 0.490 mg. per cent, hypophasic 12.00, zeaxanthin 2.45, mytiloxanthin 6.50. If the difference between normal and spawned female mussels is taken to be due entirely to the shedding of eggs, however, it is found that the decrease in carotenoid content is greater than could be accounted for in this way. Furthermore, since the sperm is not pigmented, one would not expect any loss in carotenoid due to spawning in males. Nevertheless, a loss of both epiphasic pigment and mytiloxanthin has taken place from the gonads of the fasted males. It is interesting to note that the increase in zeaxanthin which has taken place in these males is almost exactly equal to the decrease in mytiloxanthin.

Effects on General Metabolism. Lipids—Table VI, the values for which were calculated in the same way as those for Table V, shows the changes in amount of total lipid, organic acid, and non-saponifiable matter during the course of the experiments. It will be noted that the total lipid shows the same type of sexual difference, when the whole animal is considered, as does the hypophasic pigment. However, when individual tissues are examined, it is found that this difference is due almost entirely to the accumulation of organic acids in the ovaries, and presumably in the eggs. The somatic tissues of the two sexes do not differ significantly from one another, and the non-saponifiable matter likewise differs little in amount in the various tissues. It will in general be seen also that the sum of organic acids plus non-saponifiable matter is never equal to the total lipid, and is often as little as half of the latter quantity. This disparity has not been explained satisfactorily.

Fasting reduces the lipid content of the mussels, but not during the first 60 days. This is in line with the view that glycogen constitutes the principal energy store of mollusks. From 40 to 50

per cent of the total lipids and from 20 to 50 per cent of the non-saponifiable matter are lost between 60 and 150 days; about 30 per cent of the somatic organic acids of females is lost during this period, but the ovaries lose only a small fraction of their organic acids, an indication that these are deposited in the eggs, to remain isolated from the rest of the body. The males lose nearly 60 per cent of their testicular organic acids during fasting. The non-saponifiable matter shows the same trend, being lost in consider-

TABLE VI

Changes in Lipids of Mussel during Fasting, on Feeding Various Diets, and after Spawning

	Treatment	Days	No. of animals	Total lipid		Organic acids		Non-saponifiable matter	
				Soma	Gonad	Soma	Gonad	Soma	Gonad
				mg.	*mg.*	*mg.*	*mg.*	*mg.*	*mg.*
Males	Fasting	10	6	254	232				
	"	60	8	224	226	60.5	84.4	61.0	57.0
	"	150	3	141	107	37.8	35.0	33.0	30.6
	" spawned	150	3	163	94.9	47.4	41.3	41.9	26.8
	Nitzschia	150	5	154	150	37.4	49.6	41.3	36.1
	Basal diet	150	0						
	" " spawned	150	2	131	82.0	36.8	23.2	32.9	23.1
Females	Fasting	10	3	294	532				
	"	60	5	295	425	77.6	142	53.1	75.5
	"	150	4	156	264	56.7	137	41.4	46.0
	" spawned	150	4	182	154	60.0	65.5	40.0	26.8
	Nitzschia	150	1	199	346				
	Basal diet	150	5	154	185	43.5	99.4	32.0	38.0
	" " spawned	150	4	134	86.5	26.9	31.0	30.2	18.4

able quantities from all tissues of both sexes. The feeding of *Nitzschia* retards this loss of lipids from males. The feeding of the basal diet is virtually without effect in females.

Water, Protein, Carbohydrate—The water content of the tissues remains nearly constant throughout, the mean values for the somatic tissues being 83.00 ± 0.363 per cent and for the gonads 81.65 ± 0.834 per cent; the difference between the two types of tissue is not significant. The values are lower than those obtained by Dr. D. L. Fox (personal communication) on whole mussels,

owing to an inevitable loss of blood during dissection. The protein content of the tissues, expressed as 6.25 times the organic nitrogen content of the fat-extracted tissues, shows no difference with sex, and is only slightly higher in the gonads (10.6 per cent) than in the somatic tissues (9.8 per cent) after 60 days of fasting. Further fasting results in only a slight decrease in the somatic tissues though a noticeable change takes place in the gonads. In fasted animals, there is a tendency for the protein concentration to increase, although a few individuals show a marked decrease. In animals fed *Nitzschia* and the basal diet, the concentration falls sharply below the level of the fasted animals. This is likewise true in general of spawned animals, the gonads of which have very low protein concentration, regardless of sex.

Since the fat content is small compared with that of proteins, it may be assumed that carbohydrate concentration varies inversely with that of proteins. If this is true, then we may say that carbohydrates decrease in concentration in the gonads of fasted animals between the 2nd and 6th months of fasting. In the somatic tissues, there is little change in concentration; in the gonads of animals fed *Nitzschia* and the basal diet, the decrease is retarded. It appears likely also that in fasted mussels the concentration of carbohydrates in the gonads of spawned is larger than that in unspawned mussels.

DISCUSSION

Zechmeister (1937) divides vertebrates into four groups, with respect to the types of carotenoid stored; the mussel is evidently similar to animals such as the birds in that only xanthophylls are selected from the dietary supply of carotenoids available. Furthermore, there is evidence, from the relative simplicity and constancy of the qualitative picture presented by the carotenoids of the mussel, that only a few xanthophylls are selected.

These few pigments are subjected to certain transformations by the mussel, including esterification and the synthesis of the animal pigment mytiloxanthin. Some light is thrown on this synthesis by the experiments during fasting; in the fasted males, the amount of mytiloxanthin showed a progressive decrease. When the animals were fed the diatom *Nitzschia*, known to contain no mytiloxanthin, the amount of mytiloxanthin, instead of decreas-

ing, increased. Evidently some substance present in *Nitzschia* serves as a precursor for mytiloxanthin.

Further evidence of synthesis of pigment by the mussel is provided by the fact that zeaxanthin increases in amount during fasting; such an increase takes place when mussels are fed on the basal diet as well. When *Nitzschia* is fed, furthermore, zeaxanthin accumulates to a much greater extent than during fasting. Certain observations of Heilbron and Phipers (1935) are of interest in this connection; on the basis of rather scanty evidence, they postulate a conversion of fucoxanthin to zeaxanthin in the alga *Fucus vesiculosus*. Strain (1938) finds no evidence of such a change in higher plants, but, in view (1) of the presence of a substance (Pigment V, Fig. 2) resembling fucoxanthin in the mussel and in *Nitzschia*, and (2) of the report of Heilbron and Phipers that a substance resembling mytiloxanthin in some of its properties is found in *Fucus*, further chemical and physiological study of the interrelations of fucoxanthin, mytiloxanthin, and zeaxanthin should be of interest.

The most striking quantitative feature of the pigmentation of the mussel is its variation with sex. As was noted in the experimental part, both somatic and gonad tissues of females contain a higher concentration of hypophasic pigment than similar tissues of males. The association of carotenoids with sex is a common one. Most ova of marine animals are colored by carotenoids, and the corpus luteum of mammals acquired its name from the color conferred upon it by its carotenoid content. The work of Moewus (1939) indicates that the pigments crocin and crocetin are concerned with the development of motility and with conjugation in gametes of the alga *Chlamydomonas*. Sexual differences in pigment concentration are fairly common in animals (Verne, 1926) and are known in plants (Emerson and Fox, 1940).

The results of the fasting experiments permit several conclusions. First of all, it is noted that the metabolism of carotenoids is apparently not an intense one. The pigments disappear during fasting at a rate which insures that their concentration in the tissues rarely falls by any significant amount, and may even increase slightly. It appears that loss of pigment is accelerated by two factors. First, those animals fed the basal diet appear to have lost more pigment than the fasted animals. Secondly,

spawning seems to result in a loss far in excess of that to be expected from the mere removal of carotenoid in the eggs. If we assume, on the basis of most of the determinations of body weight, that the basal diet was not utilized by the mussels, while some benefit was derived from the *Nitzschia* cells which were fed, we may derive a tentative explanation of these phenomena. The feeding process, in the mussel, involves (1) production of a current of water through the mantle cavity by means of the ctenidial cilia, (2) secretion of mucus by the ctenidial cells, (3) entanglement of food particles in the mucus, with transfer of the mucus strands containing food to the mouth by the action of the cilia. Fasting mussels, living in water completely free of suspended matter, would presumably not carry on this process to any considerable extent; only a current of water sufficient for respiratory purposes would probably be produced. Feeding mussels, on the other hand, would be active continually in filtering the water and ingesting food. If they were unable to digest the basal diet, they would have no source of material to replace the substances consumed by the activities of feeding; on the other hand, by digesting and absorbing a portion of the *Nitzschia* material, they would be able to replenish these substances to some extent. It seems likely, then, that tissue carotenoids are consumed in the course of the activities associated with feeding. The association, in the vertebrates, of vitamin A with the integrity of mucous surfaces is brought immediately to mind.

The disappearance of carotenoids from the gonads of fasted animals may be taken as an indication that the carotenoids play some rôle in gametogenesis. This view-point is strengthened by the observation that the gonads act as a store of reserve carotenoids, drawn upon in fasting. The gonads also serve as a store of carbohydrate, but not of lipid, which disappears uniformly from all the tissues in fasting. In line with this last observation, it should be noted that the distribution of carotenoids is independent of that of other lipids; this is contrary to the assertion which is sometimes made (see Zechmeister (1937)) that the distribution of carotenoids in the animal body is dependent largely on their solubility in fatty substances. Both lipids and carotenoids, however, are accumulated to a considerable extent by the eggs.

SUMMARY

1. The results of a qualitative study of the carotenoid pigments of *Mytilus californianus* are reported.

2. It is found that only xanthophylls of a few types and their esters are present in the tissues of the mussel; *Mytilus* selects the xanthophylls of the food and rejects the carotenes.

3. A new acidic xanthophyll with an absorption maximum at 500 mμ is described, and provisionally referred to as mytiloxanthin.

4. Quantitative studies of the distribution of carotenoids in *Mytilus* show that the concentration of hypophasic pigments in all tissues of female mussels is higher than that of males.

5. The changes in concentration and amount of carotenoid, lipids, organic nitrogen, and water were followed during a period of 6 months, in mussels subsisting on a basal carotenoid-free diet, on a diet of *Nitzschia closterium,* and without any source of food.

6. It is found that the gonads act as a store of carotenoid and of carbohydrate, but not of lipid. The concentration of carotenoids is independent of that of lipids.

7. Prolonged fasting results in a very small loss of pigment; during fasting mytiloxanthin disappears and zeaxanthin is formed.

8. Both mytiloxanthin and zeaxanthin increase in amount when the diatom *Nitzschia* is fed; mytiloxanthin is not present in *Nitzschia.*

9. The activities of feeding and of gametogenesis are shown to be associated with an increased destruction of pigment.

10. The results of the investigation are definitely in favor of the view that carotenoids play a positive rôle in the metabolism of *Mytilus.*

BIBLIOGRAPHY

Abeloos, M., and Fischer, E., *Compt. rend. Soc. biol.*, **95**, 383 (1926).

Emerson, R., and Fox, D. L., *Proc. Roy. Soc. London, Series B*, **128**, 275 (1940).

Fabre, R., and Lederer, E., *Bull. Soc. chim. biol.*, **16**, 105 (1934).

Fischer, E., *Compt. rend. Soc. biol.*, **97**, 1459 (1927).

Fox, D. L., Marks, G. W., Austin, F. O., and Buley, H. M., *Bull. Scripps Inst. Oceanog. Univ. California Tech. Series*, **4**, No. 1 (1936).

Fox, D. L., Sverdrup, H. U., and Cunningham, J. P., *Biol. Bull.*, **72**, 417 (1937).

Heilbron, I. M., and Phipers, R. F., *Biochem. J.*, **29**, 1376 (1935).
Kuhn, R., and Sörensen, N. A., *Ber. chem. Ges.*, **71**, 1879 (1938).
Lederer, E., *Bull. Soc. chim. biol.*, **20**, 554, 567, 611 (1938).
Lwoff, A., *Bull. biol. France et Belgique*, **61**, 193 (1927).
Moewus, F., *Naturwissenschaften*, **27**, 97 (1939).
Palmer, L. S., Carotenoids and related pigments, American Chemical Society monograph series, New York (1922).
Smith, J. H. C., *J. Am. Chem. Soc.*, **58**, 247 (1936).
Strain, H., Leaf xanthophylls, Washington (1938).
Teissier, G., *Compt. rend. Soc. biol.*, **109**, 813 (1932).
Verne, J., Les pigments dans l'organisme animale, Paris (1926).
Whedon, W. F., and Sommer, H., *Z. vergl. Physiol.*, **25**, 523 (1938).
Zechmeister, L., Carotenoide, Berlin (1934); *Ergbn. Physiol.*, **39**, 117 (1937).
Zechmeister, L., and von Cholnoky, L., Die chromatographische Adsorptionsmethode, Berlin (1937).
Zechmeister, L., von Cholnoky, L., and Polgár, A., *Ber. chem. Ges.*, **72**, 1678 (1939).

Contribution No. 113

[*Reprinted from* Sigma Xi Quarterly, *Autumn Issue, 1940, Vol. 28, No. 3*]

THE UNITY OF THE SCIENCES OF THE SEA [1]

H. U. Sverdrup
Scripps Institution of Oceanography, University of California
La Jolla, Calif.

Anyone who examines a list of publications from an oceanographic institution will notice the diversity of the subjects dealt with. Let me quote a brief series of titles of such papers published in recent years:

On the mutual adjustment of pressure and velocity distributions in certain simple current systems.

Periodic changes in spectral scattering and spectral transmission of daylight in tidal water.

The relation of dissolved oxygen to nitrogen in some Atlantic waters.

Concerning the copepod, *Eucalanus elongatus* Dana, and its varieties in the northeast Pacific.

The biological approach to the preparation of anti-fouling paints.

Radium content of some inshore bottom samples in the Pacific Northwest.

This enumeration could be continued indefinitely and a more complete list of titles would leave the impression that oceanography is nothing but a wide tarpaulin spread over an exhibit of products which are labelled "marine," or that it is a bag into which are packed all subjects more or less related to the character of the ocean waters, the organisms living in the sea, the features of the ocean bottom, and those dealing with the effect of the oceans on climate and the commercial utilization of sea products.

Superficially, there seems to be no unity within the marine sciences, but the obvious reasons for this apparent conglomeration of unrelated subjects are that our comprehension has to increase step by step and that each little addition to our knowledge has to be made within a special field. Oceanography may sometime in the distant future give us a many-colored picture of the oceans, but at the present time we have only started working with a large and intriguing puzzle game, each one of us trying to put together pieces of similar color, hoping that some time all fragments can be joined into one complete picture. It is as yet far too early to guess what this picture will look like, but it is not difficult to visualize oceanography as a unified field of research.

The oceans can be considered an immense aquarium in which numerous kinds of organisms live, bacteria, microscopic plants, giant kelps, tiny primitive animals, and the largest mammals known ever to have existed on earth. In this balanced aquarium plants synthesize organic matter in the presence of light, and other forms live off the plants as is the case on land. The conditions for plant growth are therefore of the utmost importance to all of the organisms in the oceans. These conditions vary from one part of the sea to another but, generalizing, it can be stated that the ocean waters represent a weak solution of nutrient salts in which peculiarly adapted plants can thrive. The cultivation of plants without soil, experiments in hydroponics, are now attracting wide attention, and

1 "Contributions from the Scripps Institution of Oceanography, New Series, No. 113."

it may be well to remember that in the ocean plants have grown without soil as far back as the geological history of the earth goes.

The occurrence of plants is limited to the upper layers of the oceans where solar energy penetrates in sufficient quantity to make photosynthesis possible. In the open ocean the plants must float freely and must have relatively large surfaces to be able to absorb sufficient quantities of phosphates, nitrates, and other mineral salts which are dissolved in the sea water and which the plants need besides light. Thus, in the photosynthetic zone, plant nutrients are extracted from the water, but simultaneously such nutrient salts are brought back in solution by the mineralization of the tissues of decomposing plants and animals. However, some organic remains sink below the photosynthetic zone before they are decomposed and part of the essential elements are removed from the surface layers, therefore the amounts available for plant growth would be exhausted if there were no mechanism for replenishment. Such a mechanism exists, because in the deeper water where no plants extract the nutrients a storage supply is maintained from which replenishment of the nutrients in the surface layers, or what one may call fertilization of the ocean pastures, is provided wherever subsurface water is brought to the surface either by ascending motion or by processes of mixing which extend to great depths. Large-scale ascending motion of subsurface water takes place along the west coast of the greater part of the American continents, along the west coast of South and North Africa, and to a more limited extent in other regions. Vertical mixing reaching to great depths occurs in high latitudes, and the areas here mentioned are the best ocean pastures, showing large populations of organisms in contrast to the open ocean regions in middle latitudes. It is characteristic that the great commercial fisheries exist in localities where relatively rapid replenishment of the plant nutrients of the surface layers takes place.

If the ocean is compared to an enormous aquarium, oceanography represents the science dealing with the functioning of this aquarium. The physical oceanographer has to account for the ocean currents which maintain an exchange of water between the different parts of the sea and he has to examine the slow ascending motions and the processes of mixing by means of which plant nutrients are brought to the surface layers. These studies correspond to studies of the stirring of the aquarium waters which provide for the fertilization of the top layers. The physical oceanographer also has to account for the mechanism by which the ocean waters are heated or cooled and by which the average temperature in different regions is kept constant, or, in other words, he has to provide information as to the thermal characteristics of the aquarium. He has to examine the penetration of light in the sea and to establish what wave lengths and what amounts of radiation reach the different depths in the different parts of the ocean. When dealing with these and similar questions the physical oceanographer need not be concerned with the populations of the ocean, but he should not forget that his work is part of a large-scale approach to an understanding of all events in the sea.

The chemist can furnish data which greatly help in the study of the origin and distribution of the water masses and the character of the currents, and data which have bearing upon the characteristics of the ocean waters as a weak solution of

nutrient salts. He faces a number of difficulties because sea water is a highly complex solution in which some salts are present in relatively high concentrations and others in minute quantities, and the study of the chemistry of sea water therefore requires special skill and accuracy, regardless of how results are applied. During the early history of oceanography emphasis was placed on the type of chemical knowledge which was applicable to problems in physical oceanography, but lately those which have bearing on biological problems are advancing more and more to the foreground.

The biologist is confronted with an unlimited number of problems because the biological sciences will naturally occupy the center of the field when the aquarium picture is used. The numerous kinds of organisms inhabiting the sea have to be known—from bacteria to whales. Their reactions to changing environments, their feeding habits, and methods of reproduction have to be examined. Studies of the complicated life histories characteristic of many marine organisms are essential in order to recognize the early developmental stages of common forms. I may remind you of one of the most dramatic episodes in oceanography, the hunt for the spawning grounds of the Atlantic eel, which started when a transparent flat creature was recognized as the larval form of the eel and which ended when it was shown that all these larvae drifted out from the Sargasso Sea to which the mature eels had migrated in order to spawn and die.

When the sea is considered as a big aquarium the ecology must receive great attention. In many cases one can deal with groups of organisms without emphasis on the individuals and without consideration of species represented in the populations. The interrelations of these groups become matters of major importance owing to the destructive competition for food which is met with everywhere in the sea.

In most marine biological problems knowledge derived from work in physical and chemical oceanography is indispensable. This is particularly true when dealing with ecological questions which cannot be answered without consideration of the environment of the organisms. I am here using the term environment in a broad sense, including the temperature of the water, the total salt content, the state of motion, the amounts of plant nutrients, the oxygen and the carbon-dioxide content of the water, the presence of other organisms than the group under consideration, and many other factors.

The geologist has to deal with the bottom of the aquarium and to study problems relating to the types of sediments found in different regions and the processes of sedimentation. He must be familiar with the mechanism by which sediments can be transported, he must know the sources of different sedimentary material, and must be acquainted with the early transformation of sediments by the activity of organisms. The study of sediments therefore requires knowledge of the state of motion of the water and of the type of organisms whose skeletal structures contribute to the formation of the bottom deposits, and it also necessitates knowledge of the chemistry of sea water and the conditions favoring solution or precipitation of such substances as calcium carbonate and silica.

Thus, the picture of the oceans as a big aquarium unites all the different branches of oceanography under a common point of view and makes evident the interrelation between the apparently separate marine sciences.

One may now ask if the unity of the sciences of the sea stops here. Do we who are engaged in studies of special functions of this aquarium have nothing in common but our distant goal? Or is it possible to point out methods of attack which are similar within the different branches so that we have not only a common goal but are also advancing along similar lines? My answer to these questions is that a number of the methods of approach are similar and that the unity of the sciences of the sea is much greater than may appear from the comparison with an aquarium.

In the first place, it should be stressed that the marine sciences essentially deal with conditions in nature and have, therefore, to be based upon observations of events in nature and not upon laboratory experiments or theoretical considerations. Controlled experiments and theoretical researches are necessary, but it should always be borne in mind that such studies are auxiliary and should be planned to facilitate the understanding of what is observed or may be observed in nature. Experiments and theories are tools without which we cannot expect to disentangle the complicated events in nature and arrange them in logical sequence. We should be helpless without tools but we would not study oceanography if data from the sea were lacking. Every oceanographic laboratory has to face the sea and every oceanographer has to go to sea!

Turning to the sea, let me draw attention to the fact that in all branches of oceanography the concept of an average steady state has found wide application. This concept is based on the experience that observations of conditions in the ocean conducted over a long period of time and in a large enough space do not show a continuous change, but demonstrate that, on an average, time changes in any given locality disappear. Superimposed upon such a steady state are periodic fluctuations related to the changes from day to night, or to seasonal changes, and superimposed are also what we call random fluctuations which, however, never continue to alter conditions in the same direction during a long time-interval, but always revert towards the average state. I shall return to the matter of periodic and random fluctuations, but wish first to discuss the importance of the concept of a steady state.

Detailed knowledge of the average steady state is in itself not important because the ultimate goal of oceanography is the same as that of all natural sciences: to predict coming events, and prediction has to be based on knowledge of processes and not on a description of unchanging conditions. However, we are not dealing with static conditions but with a delicate dynamic equilibrium which is maintained by opposing factors, and we are studying the steady state in order to gain knowledge of these factors. If some of them can be observed, others may be determined indirectly because we know that on an average their effect must balance the effect of the observed ones. Thus, the concept of a steady state receives its importance when one realizes that it implies the concept of a state of dynamic equilibrium.

The application of this principle of dynamic equilibrium can be illustrated by a number of examples. Consider first the heat budget of the oceans. This heat budget is exactly balanced, meaning that the amount of heat received by the oceans exactly equals the loss of heat from the oceans. The amounts of heat conducted from the interior of the earth can be disregarded because it is negligible

compared to that received by absorpton of short-wave radiation from the sun and the sky and by absorption of long-wave radiation from the atmosphere, or lost by long-wave back radiation. All processes of radiation combined lead to a gain of heat which can be measured with considerable accuracy, and which must equal the loss by conduction of sensible heat to the atmosphere and by evaporation. The amount which is lost as sensible heat can be approximately estimated and, thus, a foundation exists for computing the average amount of evaporation from the surfaces of the ocean. Such computations based entirely on the concept of heat balance have led to the conclusions that the average evaporation from all oceans amounts to very nearly 100 cm. per year (39 inches). This result represents a valuable check on directly measured values which have to be subjected to a number of uncertain corrections.

As another example of the application of the same principle, let us consider the currents through the Strait of Gibraltar which connects the Mediterranean Sea with the open Atlantic Ocean. In the Mediterranean Sea evaporation greatly exceeds precipitation and runoff, and there must, therefore, be a net inflow of Atlantic water into the Mediterranean Sea in order to compensate for the water lost by excess evaporation. On the other hand, the net salt transport through the Strait of Gibraltar must be zero because, otherwise, the salinity of the Mediterranean waters would decrease or increase. Now, the Atlantic water which flows in is of high salinity, about 36.2 per mille. If the net transport of salt shall be nil Mediterranean water of even higher salinity must flow out along the bottom, but the amount of water flowing out must be smaller because a fraction of the inflowing Atlantic water has evaporated. Observations in the Strait of Gibraltar indicate that this is exactly what happens, but the data are incomplete, for which reason the concept of a dynamic equilibrium greatly helps the interpretation of the observations and the understanding of the processes which operate. On an average, about 36.3 cubic miles of Atlantic water flow into the Mediterranean every 24 hours and 34.9 cubic miles of Mediterranean water flow out. The difference between these amounts, about 1.4 cubic miles per day, represents the excess of evaporation over precipitation and runoff.

So far, my examples have been taken from the field of physical oceanography, but in order to support my contention that the same principle is generally applicable, I have to present examples from other fields. Let us, therefore, examine the distribution of oxygen in the ocean. The oxygen which is present in the sea has either been absorbed from the air at the sea surface or it has been produced in the surface layers by the photosynthetic processes of plants. In the surface layers the water is generally saturated with oxygen but at greater depths lower oxygen values are found, because there oxygen is being removed from the water by the respiration of organisms or is utilized in some other manner for oxidation of organic matter. Studying the distribution of oxygen in the deep water one finds, however, that it varies widely from one locality to another, and a minimum oxygen layer which is found at an intermediate depth in most oceans has attracted wide attention. When discussing the general distribution of oxygen it should again be borne in mind that, on an average, a state of dynamic equilibrium exists, meaning that if observations are repeated one will always find nearly the same amount of oxygen present at a given point. Certain seasonal variations may be found but

averages based on observations in different seasons and different years will not show any tendency to change in a constant direction. At any point replenishment of oxygen takes place by processes of mixing or by horizontal currents, and consumption of oxygen takes place by oxidation of organic matter. On an average, replenishment must exactly balance consumption because, if that were not the case, the amount of oxygen in the locality under consideration would either decrease or increase. On the basis of this principle of dynamic equilibrium some idea has been obtained of the actual oxygen consumption within the different parts of the ocean. This has not been measured by studying the biological processes which take place but by computing the replenishment on the basis of knowledge of mixing and currents, and the values for the replenishment have been considered representative of the consumption which, in the examined regions, has been found to be of the order of one milliliter of oxygen per liter of sea water per year.

Let us examine still another question. It has been found that the ocean waters, in general, contain small amounts of dissolved organic matter. The amounts are so small that their presence is best demonstrated by the fact that sea water collected from any depth is capable of furnishing nourishment for a population of heterotrophic bacteria if such conditions are created that the bacteria can develop. The procedure used in these determinations is to saturate a number of water samples from a certain depth with oxygen and determine the amount of oxygen consumed by the bacteria. It has repeatedly been found that the populations of bacteria will increase to a certain limit and will consume a definite amount of oxygen. It is assumed that the oxygen thus consumed is used for oxidation of part of the organic matter which was originally present in the water, and from the total amount of oxygen consumed one can compute how much of the organic matter in the sea water has been utilized by the bacteria. The amounts determined in this manner are of the order of 5 milligrams per liter of water, meaning that the concentration of the organic matter is at least five parts in one million.

On the basis of these findings certain speculations can be advanced. Laboratory experiments show that bacteria can reduce the concentration of organic matter in sea water to values as low as one part in one hundred millions. Why, then, do not the bacteria in the sea reduce the concentration existing there below five parts in one million? The answer appears to be that when a sample of sea water is enclosed in a bottle organic matter is absorbed by the surface of the bottle and thereby becomes available to the bacteria adhering to these surfaces, whereas in the deep ocean where no solid surfaces exist the bacteria cannot utilize all the organic matter present. But why should the limiting concentration be about five parts in a million and not fifty parts in a million or one part in ten millions? The answer is perhaps that we have again a state of dynamic equilibrium at which the replenishment of dissolved organic matter equals the consumption by bacteria, the latter being partly controlled by existence or non-existence of solid surfaces to which the bacteria can adhere. In this case none of the factors which maintain the balance are known, but the principle of dynamic equilibrium helps towards clarifying the problems involved and towards developing methods of attacking these problems.

This principle of a dynamic equilibrium can also be applied on a large scale to the different types of populations in the sea. The average quantity of phytoplankton, of the different forms of zooplankton, and even of the different species of fishes and of the large mammals of the sea, remains unaltered owing to the competition between the different groups. It is true that the existing balance is occasionally seriously interfered with by the activity of man, but over a long period of time his activity will be governed by similar laws of competition because his efforts towards utilizing to the utmost certain species of fishes or such mammals as the whale, will depend upon his economic return. When the fish becomes scarce his efforts will diminish and a new state of equilibrium will be reached which is characterized only by the fact that man has joined the group of aquatic beasts of prey.

I may add that the sea is far from being a régime of peaceful negotiations. To the contrary, it is difficult to visualize any region in which there is more cutthroat competition between species than there exists in the ocean, or a region in which a balance between species is maintained by more rigorous means. One has to consider not only the competition between the different species but also the difficulties encountered by the organisms of the sea owing to the very character of the environment. I may mention the fact that many marine organisms have no means of locomotion but are, throughout their life-span, carried by ocean currents and are unable to secure for themselves more suitable environmental conditions, and that many organisms during some stage of development are similarly transported helplessly by the moving water masses. No wonder that most marine organisms are prolific in their production of offspring because few have a chance to survive and reach maturity!

I have pointed out that the concept of a dynamic equilibrium is helpful in understanding the aquarium with which we deal, and that this concept can be used successfully when applied to a large number of oceanographic problems. However, such a principle is by no means characteristic of the marine sciences only, because it is useful in many other instances as well. It has found application to ecological problems in zoology and botany, in climatology and other natural sciences, and even in the field of social science. There exists, however, another principle which finds its widest application within oceanography, that which is based on the fact that the waters of the ocean represent a continuous medium, for which reason all events in the sea must follow the laws characteristic of a continuous medium.

When dealing with the dynamic equilibrium, emphasis is placed exclusively on what happens in a given locality, and the definition of a steady state is that time-changes in a given locality are zero. In the ocean it is necessary, however, to distinguish between what happens in a given locality and what happens within an individual water mass which is in constant motion from one locality to another. When dealing with the heat budget of the ocean it was stated that on an average the gains and losses of heat are equal, but this applies to the ocean as a whole, and the heat content of an individual water mass may be subject to great changes. In physical oceanography one distinguishes between the local and the individual changes, and such distinctions will be helpful in many other cases and will prevent erroneous conclusions. Let me take an example from the field of sedimenta-

tion. On a wide continental shelf the coarsest sediments are found near the coast and near the outer border of the shelf, whereas finer sediments are found between these regions. It may be concluded that the finer sediments are being deposited on the middle part of the shelf, but the observed distribution can exist even if no net deposition of sediments takes place anywhere on the shelf. There may be a steady transport of finer sediments from the regions near the coast and across the border of the shelf. Finer particles brought from the coast may be deposited at some distance offshore, but in the localities where they are deposited other particles are picked up by moving eddies and carried farther out. These are deposited somewhere else and new particles are picked up, and so on until, finally, an amount passes the outer border of the shelf equal to the amount which was added near shore. Thus we have a steady state without any net deposition, but each individual particle is more or less on the move, and where it will come to rest cannot be predicted.

When dealing with biological phenomena it is particularly important to be aware of the difference between local and individual changes. Observations of phytoplankton at a fixed locality often indicate sudden changes in the amount of phytoplankton present. It may be concluded that the rate of reproduction of the phytoplankton has suddenly changed or that the rate of grazing has suddenly increased, but such conclusions are invalid unless it can be shown that no new water-mass has entered the area. One has to remember that the water is in motion, that sharp transitions often exist between different types of water and that local changes may be due to intrusion of a new water-mass and not to the operation of local factors.

The concept of the continuity of the ocean waters and the consequences of that continuity has only in part found application to biological problems, but I am convinced that it will enter more into the foreground and that it will become a powerful tool characteristic of all the marine sciences.

When leaving the examination of the average steady state we have to realize, in the first place, that changes may be caused in part by agencies which operate locally and, in part, by factors which were in operation somewhere else but are felt in our locality owing to the state of motion of the water. Let me take a somewhat extreme example. During the past winter considerable damage was done along beaches in the Los Angeles district, particularly at Santa Monica and Redondo Beach, where numerous structures were destroyed by exceptionally large waves. The destruction caused considerable excitement, and in the press it was suggested that these destructive waves were due to some "mysterious submarine force." However, the reported waves were surface waves of periods often observed in the region but of unusual height, and they occurred on each occasion after a severe storm in the North Pacific. I do not doubt for a moment that they were ordinary swells created by strong winds at sea which, owing to the configuration of the coast, were more severely felt in some localities than in others. These swells are comparable to those which frequently damage the Atlantic coast of Morocco and prevent the loading and unloading of vessels anchored at open roadsteads. For years these heavy swells have been forecast on the basis of reports of strong persistent winds over the central part of the North Atlantic. We have here examples of local events which occurred as a

result of factors which were operating at a great distance from the place where the events were actually observed.

Diurnal and annual fluctuations may similarly be attributed to factors operating locally or at a distance. These fluctuations are repeated in a regular manner and, by accumulation of data, one can learn how the different factors involved operate, not only towards producing periodic changes but also towards maintaining the steady state. Principally, the methods to be employed are the same within all branches of marine sciences, because in all events we have to take into consideration that we are dealing with a continuous medium.

The periodic events, the annual march of temperature, the annual cycle of the phytoplankton, or the annual arrival of fish to spawning grounds, represent fascinating objects of study, but the cases of abnormal development are often even more fascinating because they may throw light over the problems. Let me again make use of an example. In recent studies of the sardine, which is caught in enormous quantities off the west coast, the question of the occurrence of dominant year-classes has been the object of considerable discussion. The fisheries investigations in northwestern Europe have shown that in certain years the spawning of the herring is very successful and that large quantities of the herring caught over a number of years were born in the same year, say, in 1929. The following years may have added little to the stock, but suddenly a new large group of mature herring of the year-class, say, 1934, may appear. The determination of year-classes is mainly based on the age of the herring, which can be found by counting the rings on the scales or on the otoliths.

Something similar seems to take place here on the west coast although the methods for establishing the existence of year-classes are not so direct. It has been demonstrated, however, that years of successful and unsuccessful spawning exist, and it was recently shown that years of successful spawning coincide with years of high temperature in the coastal waters. Now, years of high temperature are also years of high sea-level on the California coast. It is, of course, possible that high temperature might be advantageous to the spawning of the sardine, but it is not conceivable that the spawning of the sardine should be affected by changes of sea-level, particularly because the differences between succeeding years rarely exceed one or two inches. It appeared, therefore probable that both the temperature and sea-level indicate some other factor which may influence the success of spawning, and it is not difficult to point to such a possible factor. The spawning of the sardine takes place at some distance from the coast, but in order to develop, the young sardine has to be brought in to the coastal waters. High temperature and high sea-level on the coast are characteristic of years in which numerous eddies of offshore water approach the coast, and the success of spawning may, therefore, be related to the type of circulation. The result of the spawning may be good in years during which the character of the current facilitates the transport of the fry and the young sardines from the offshore spawning grounds to the coastal waters. Here we have an example of an event which is not periodic, but for that very reason may lead to the understanding of processes which are in operation every year but which appear conspicuously in a few years only.

This last example also serves to emphasize how closely the many events in our big aquarium are related to each other and how necessary it is to have available information from many branches of marine sciences in order to understand what

happens. It is, however, fortunate that in many instances it is sufficient to examine a small portion of the aquarium, neglecting the fact that all ocean waters are in communication with each other. If we stretch a point we may say that the waters of the Black Sea are in communication with those of the Antarctic Ocean through the narrow straits of the Bosporus and Dardanelles through the Mediterranean Sea, the Strait of Gibraltar, and the North and South Atlantic Oceans, but for all practical purposes the waters of the Black Sea are isolated from the rest of the oceans and the Black Sea represents an independent aquarium. Thus, one can introduce the concept of "degree of isolation" which is very useful when considering the characteristics of any given region. The isolation may be in a horizontal direction due to land barriers or submarine ridges, or it may be in a vertical direction due to the existence of layers within which the density increases so rapidly that no vertical mixing can take place. As an illustration let us consider one of the oyster basins in western Norway where in summer the water-masses in the basin are isolated both horizontally and vertically. These small basins open towards the sea through narrow and shallow channels and in winter are filled by water of relatively high salinity. In the spring a nearly fresh-water top layer is formed by runoff, and this surface layer is of such low density that the deeper water becomes completely isolated because it cannot flow out over the shallow sill, and it does not mix with the much lighter brackish water on top. This isolation leads to characteristic consequences. Part of the solar radiation penetrates through the upper fresh layer and is absorbed in the deeper water in which the temperature increases abnormally because the fresh top layer prevents contact with the atmosphere and thus prevents any loss of heat. The layer of brackish water is often less than six feet thick and may attain in summer a temperature of about 65° Fahrenheit, but by absorption of radiation the temperature below a depth of six feet may be raised to 90° Fahrenheit, and in this warm water oysters which cannot live on the open coast of Norway will thrive and spawn. In winter the deep water is mostly renewed, but if renewal does not take place the oxygen content of the water will be consumed and stagnant water will develop in which no organisms can live except anaerobic bacteria. Such isolated and stagnant deep water without oxygen fills the entire basin of the Black Sea.

The question of the degree of isolation is one which has to be examined when any particular region is selected for intensive study. It is again fortunate that even in the open ocean one need not always take into consideration the entire body of water between the surface and the ocean bottom, because in lower and middle latitudes the circulation within the upper 600 to 800 meters is nearly independent of the deep-water circulation, and a nearly horizontal boundary surface separating two different oceanographic régimes can be established. Vertical boundaries can also be established on oceanographic principles. Coastal waters in middle latitudes are often characterized by lower salinity and greater annual variation of temperature than the oceanic waters in the same latitude. Upon leaving the coast one will mostly observe an increase of the salinity of the surface layers and a decrease of the annual range of temperature, and the boundary of the coastal water can be placed in the region in which no further increase of salinity- or decrease of temperature- range takes place. With due consideration of mixing at this boundary the coastal waters can be dealt with as a separate body of water

which, to a great extent, is under the influence of local factors. In each individual case the oceanographic boundaries to be selected depend upon the character of the region and the problems to be examined, but it must always be borne in mind that introduction of such boundaries also means introduction of boundary conditions which must be fulfilled. As an illustration, let me mention that no net transport of salt can take place through any boundary surface in the sea.

When dealing with the deep-water circulation of the ocean the interdependence of all oceans has to be realized because the deep water of all oceans is formed in the Antarctic and to some extent in the Arctic, and is, therefore, of similar character all over the world. Off the American west coast one does not need to travel five thousand or more miles towards the south in order to find Antarctic water. Antarctic water is much closer because samples of such water can be brought up from depths of about one mile.

A study of the deep-water circulation of the oceans requires data from all seas and necessitates extensive cooperation between institutions of many countries, but otherwise every oceanographic station can select its own region for intensive study and can define the limits of the region according to its general program. Thus, we can subdivide our aquarium and so are not facing the hopeless task of having to examine the entire body of water of the oceans, all of the 330 millions of cubic miles of water, in order to understand all the events in the sea. It is rational to advance step by step and to deal with specific regions and specific questions related to that region in order gradually to build up the complete picture. From this point of view the titles of papers which I quoted as an introduction do not show oceanography as a conglomeration of unrelated subjects, but present on the contrary an example of the detailed work which is necessary in order to build up our knowledge of the oceans. Varied as the list was it bears evidence not of scattered efforts but of the unity of the sciences of the sea.

References

Fleming, R. H., and Roger Revelle, Physical Processes in the Ocean. In: Recent Marine Sediments, A Symposium, pp. 48-141, A. A. P. G., Tulsa, Oklahoma, 1939.

Gaarder, T., and R. Spärck, Hydrographisch-biochemische Untersuchungen in norwegischen Austern-Pollen. Bergens Museums Arbok 1932, Naturvidenskapeligrekke, Nr. 1, pp. 5-144.

Mosby, H., Verdunstung und Strahlung auf dem Meere. Ann. d. Hydrographie und maritimen Meteorologie, vol. 54, p. 281, 1936.

Revelle, Roger, and F. P. Shepard, Sediments Off the California Coast. In: Recent Marine Sediments, A Symposium, pp. 245-82, A. A. P. G., Tulsa, Oklahoma, 1939.

Schott, Gerhard, Die Wasserbewegungen im Gebiete der Gibraltarstrasse. Conseil Perm. Intern. pour l'Exploration de la Mer, Journal du Conseil, vol. 3, pp. 139-175, 1928.

Seiwell, H. R., The Minimum Oxygen Concentration in the Western Basin of the North Atlantic. Papers in Physical Oceanography and Meteorology, vol. 5, pp. 24, 1937.

Wüst, Georg, Die Verdunstung auf dem Meere. Veröff. des Inst. für Meereskunde an der Universität Berlin. N. F., A., Heft 6, 1920.

Zobell, C. E., The Effect of Oxygen Tension on the Rate of Oxidation of Organic Matter in Sea Water by Bacteria. Journal of Marine Research (in press).

Contribution No. 114

BACTERIOLOGICAL ANALYSIS OF SOME LONG CORES OF MARINE SEDIMENTS

By

SYDNEY C. RITTENBERG

Scripps Institution of Oceanography [1]
University of California
La Jolla, California

Until recently only the uppermost layers of marine sediments have been generally available for scientific investigations since most coring instruments obtained samples less than a meter long. The early bacteriological investigations of Certes (1884), Russell (1892), Fischer (1894), Gazert (1912), and Drew (1912) were confined to surface samples obtained by dredging. Lloyd (1931) was the first to report quantitative data on the vertical distribution of bacteria in subsurface layers of marine sediments. Similar investigations were made by Reuszer (1933), and Waksman et al. (1933). ZoBell and Anderson (1936) and ZoBell (1938) enumerated both aerobic and anaerobic bacterial populations. The longest core on which quantitative results have been published was 68 centimeters long (ZoBell and Anderson, 1936) although Waksman et al. (1933) have reported the occurrence of anaerobes down to a depth of 90 centimeters.

There are certain problems whose solutions require information on the depth to which bacteria may be present and active in marine sediments. For this reason the bacteriological analysis of as deep strata

[1] Contributions from the Scripps Institution of Oceanography, New Series No. 114. Technical assistance was furnished by the personnel of Works Progress Administration Official Project No. 665-07-3-141.

Reprint from SEARS FOUND. JOURN. MAR. RES.

as possible is desirable. As an example of such problems it is sufficient to mention the controversy over the role of bacteria in petroleum genesis; certain geologists believe bacterial activity is limited to an initial period before the source material is buried deeply (White, 1935), while others believe bacteria remain active during the entire process (McCoy and Keyte, 1934).

Emery (1939) developed a heavy gravity coring tube which is a greatly enlarged modification of the Ekman (1905) mud sampler. Through the cooperation of Dr. F. P. Shepard and Dr. R. Revelle several cores of considerable length, obtained with this instrument on cruises of the "E. W. Scripps" were made available for bacteriological analysis. The results of these analyses are the subject of the present paper.

EXPERIMENTAL

The coring device consists of three principal parts: an upper iron pipe on which 200 to 500 pounds of streamline lead weights are placed; a valve to prevent loss of the core; and a lower iron pipe two inches in diameter and six to twenty feet long, the length used depending on the type of sediment expected. A special nose used on the end of the lower pipe serves to decrease the frictional force between the inside of the core tube and the mud. This instrument has taken cores up to 370 centimeters in length and has been used successfully in water over 4000 meters deep. The apparatus has actually penetrated as much as 770 centimeters into the sediment, but because of frictional forces a smaller and smaller percentage of each succeeding layer is collected as the corer moves through the mud (Emery and Dietz, 1939). Consequently the depth of the sample below the surface of the core as used in the following discussion and tables does not represent the actual depth below the surface of the sediment *in situ*. The actual depth will be greater than that reported by an amount depending in part on the ratio of the length of penetration of the core barrel to the length of core recovered, and in part on the nature of the sediment itself.

Usually the sediment was removed from the core tube immediately after being brought on board the vessel and cut into three- to five-inch sections which were stored in glass-covered pint jars. Samples for bacteriological analysis were obtained by dissecting out a radially central portion of mud from the inside of the freshly cut sections, using aseptic technique during all manipulations. These sub-samples were stored in sterile tubes or bottles in a refrigerator at 0° C. until returning to the laboratory on shore where the analyses were made. Core F 72, however, was analyzed on board immediately after it was obtained.

Ten grams of the sediments were weighed into tared dilution bottles

containing 90 cc. of sterile sea water. The bottles were then shaken vigorously for at least five minutes to obtain a uniform suspension. One-cc. portions of appropriate dilutions of the suspension were used to inoculate Petri dishes to determine the aerobic population, and oval tubes (Rittenberg et al., 1937) to determine the anaerobic population. A 1 : 100 dilution was the lowest used in making aerobic counts. If no colonies developed on either plate inoculated with this dilution the count was recorded as <50. A nutrient medium of sea water plus 0.3 per cent bacto-peptone, 0.2 per cent each of proteose-peptone and beef extract, 0.025 per cent $FeCl_3 \cdot 6H_2O$, and 1.5 per cent agar at a pH of 8.0 was used. The inoculated plates and oval tubes were incubated at 20° C. for two to four weeks before the colonies were counted.

All the samples examined, with one exception, were terrigenous deposits (Murray and Renard, 1891). According to the system of classification in use at the Scripps Institution (Revelle, 1940) these sediments are green clays or silts. Their median particle diameters vary from core to core and within individual cores, ranging from 2.5 to 44 microns. Their water contents vary with depth of burial and particle size, ranging between 30 and 70 per cent. Their organic nitrogen content falls between .10 and .32 per cent. The one pelagic deposit examined, F 72, consists of red clay overlying a very fine, dry, gray-green clay. Its median diameter ranges from 2.5 to 3.5 microns.

Bacteriologically the nine terrigenous samples roughly fall into three groups characterized respectively by high, intermediate, and low bacterial populations. This classification does not give a sharp separation because certain of the cores might be placed in either of two groups, depending on the portion of the data stressed. The terms high and low populations refer only to the ranges observed in this investigation and are used merely for convenience in discussing the data; it should not be inferred they delimit the maximum and minimum possible bacterial contents of terrigenous sediments.

Table I shows the number of bacteria demonstrated at various levels in cores of green mud of intermediate population. The number of aerobes in the topmost layer is high, ranging between one million and eight million per gram wet weight. Immediately below the surface of the mud the number of bacteria found decreases rapidly, less than 10,000 per gram being present at a depth of 20 centimeters. Very few bacteria develop from sediment layers 70 centimeters or more below the surface, the number, with one exception, being below 500 per gram. A characteristic shown by FPS 149 which is common to almost every core examined is that at all levels the aerobes are more numerous than

the anaerobes. Only 1,500 anaerobes per gram were demonstrated at the surface of FPS 149; the number found dropping to less than 500 per gram in the first 30 centimeters and remaining very low throughout the rest of the core. It is unfortunate that the anaerobic populations of the other two cores were not determined.

Table II shows the vertical distribution of bacteria in two cores of green mud of low population. The cores in Table II are separated from those in Table I only because of the large differences in the aerobic population of the surface layers. In the deeper portions the numbers and vertical distribution of bacteria in the two groups of cores are quite similar.

The results of the counts on sediments of high population are given in Tables III and IV. In these cores the numbers of aerobes and anaerobes in both the surface and subsurface layers are considerably higher than in the cores discussed above. At the surface the counts are as much as tenfold greater and in the lower layers there are differences up to ten thousandfold. Core FPS 253 might have been included in the intermediate group but because of the large number of bacteria at the surface it is also considered a sediment of high population. It

TABLE I

NUMBER OF AEROBIC AND ANAEROBIC BACTERIA PER GRAM OF WET SEDIMENT DEMONSTRATED IN DIFFERENT STRATA OF CORES OF GREEN MUD OF INTERMEDIATE POPULATION

Sample	FPS 149		39-C-39		39-C-40A	
Location of station	32° 36.4′ N. 117° 27.8′ W.		33° 02.5′ N. 118° 01.5′ W.		33° 04.5′ N. 117° 55.5′ W.	
Depth overlying water	1190 meters		935 meters		916 meters	
Time stored before analysis	12 hours		4 hours		4 hours	
Depth of sample below surface of core in cm.	*Bacteria per gram* *aerobes*	*anaerobes*	*Depth of sample below surface of core in cm.*	*Bacteria per gram aerobes*	*Depth of sample below surface of core in cm.*	*Bacteria per gram aerobes*
0–2	7,500,000	1,500	0–3	1,850,000	0–2	2,415,000
2–5	250,000	2,250	3–8	230,000	2–5	55,000
5–9	200,000	7,200	8–18	2,900	5–8	15,800
9–13	100,000	1,350	18–28	600	10–12	800
18–22	20,000	470	48–58	<50	20–22	150
28–43	3,300	5	79–89	2,150	36–38	50
43–58	2,100	80	109–119	400	53–55	<50
58–74	100	10	137–150	50	74–76	400
74–89	200	10	170–180	250	91–94	<50
89–104	150	45				
104–119	150	10				
119–134	50	5				
134–149	100	5				
149–165	<50	0				
165–180	150	5				
180–196	200	5				

TABLE II

NUMBER OF AEROBIC AND ANAEROBIC BACTERIA DEMONSTRATED IN DIFFERENT STRATA OF CORES OF GREEN MUD OF LOW BACTERIAL POPULATION

Sample	39-C-1		39-C-4	
Location of station	32° 55.7′ N. 117° 36.8′ W.		33° 03.3′ N. 117° 25.5′ W.	
Depth overlying water	935 meters		465 meters	
Time stored before analysis	8 hours		6 hours	
Depth of sample below surface of core in cm.	*Bacteria per gram of sediment (wet weight) aerobes*	*anaerobes*	*Depth of sample below surface of core in cm.*	*Bacteria per gram of sediment (wet weight) aerobes*	*anaerobes*
0–5	180,000	7,500	0–3	240,000	17,500
5–17	60,000	6,500	3–8	155,000	12,000
30–43	1,100	30	33–46	300	10
56–69	50	0	71–76	350	65
81–94	100	0	109–122	50	0
145–158	<50	0			
185–198	<50	0			
211–224	100	0			
236–249	<50	0			

should be noted that the cores in this group were stored between 60 and 110 hours before analysis while those in the other two groups were all stored less than 12 hours.

Within certain cores the vertical distribution of bacteria departed from a general decrease in numbers with depth by a significant amount. In the two most striking examples observed (Table IV) the occurrence of layers of high population below layers of low population was associated with discontinuous changes in the physical properties of the sediment. In FPS 258, 270,000 bacteria per gram were found at a depth of 303–313 centimeters below the surface, while the number of bacteria in the layers above and below this depth was considerably

TABLE III

NUMBER OF AEROBIC AND ANAEROBIC BACTERIA DEMONSTRATED IN DIFFERENT STRATA OF CORES OF GREEN MUD OF HIGH BACTERIAL POPULATION

Sample	FPS 251		FPS 253	
Location of station	36° 13.0′ N. 121° 55.1′ W.		34° 49.0′ N. 121° 10.0′ W.	
Depth overlying water	676 meters		530 meters	
Time stored before analysis	108 hours		84 hours	
Depth of sample below surface of core in cm.	*Bacteria per gram of sediment (wet weight) aerobes*	*anaerobes*	*Depth of sample below surface of core in cm.*	*Bacteria per gram of sediment (wet weight) aerobes*	*anaerobes*
0–12	23,800,000	290,000	0–10	18,300,000	110,000
12–25	138,000	26,000	10–15	4,000	1,100
51–64	63,000	3,100	55–67	4,200	45
102–115	24,000	4,800	107–120	400	95
127–140	23,000	4,700	142–155	100	40

TABLE IV

NUMBER OF AEROBIC AND ANAEROBIC BACTERIA DEMONSTRATED IN DIFFERENT STRATA OF CORES OF GREEN MUD SHOWING ZONES OF HIGH POPULATION BENEATH ZONES OF LOW POPULATION

Sample	FPS 258		FPS 259	
Location of station	34° 14.0′ N. 120° 02.5′ W.		34° 11.8′ N. 120° 02.0′ W.	
Depth overlying water	566 meters		565 meters	
Time stored before analysis	60 hours		60 hours	
Depth of sample below surface of core in cm.	*Bacteria per gram of sediment (wet weight) aerobes*	*anaerobes*	*Depth of sample below surface of core in cm.*	*Bacteria per gram of sediment (wet weight) aerobes*	*anaerobes*
0–5	3,050,000	232,000	0–18	15,800,000	272,000
5–13	11,700,000	189,000	18–31	9,100,000	178,000
25–38	3,275,000	54,000	56–79	788,000	2,660
76–89	2,300,000	15,000	107–120	2,600	330
152–165	43,000	9,600	157–170	17,000	200
228–231	8,400	18,000	232–245	102,000	390
303–313	270,000	42,000			
342–355	15,000	2,200			

lower. A similar zone of high population was observed 232–245 centimeters below the surface in FPS 259. In exactly these same layers there was a very abrupt increase in the water content and decrease in the cohesiveness of the sediment. The zone of relatively high population at 78–89 centimeters depth in 39-C-39 has not as yet been correlated with an abrupt change in any other characteristic of the sediment.

Table V shows the numbers of bacteria found in the various layers of the only pelagic deposit examined. The numbers of aerobes and anaerobes were uniformly low throughout the length of the core with a maximum at the surface.

TABLE V

NUMBER OF AEROBIC AND ANAEROBIC BACTERIA DEMONSTRATED IN VARIOUS STRATA OF A CORE OF PELAGIC SEDIMENT

Sample	F 72	
Location of station	30° 25.0′ N. 118° 32.5′ W.	
Depth overlying water	3005 meters	
Depth of sample below surface of core in cm.	*Bacteria per gram of sediment (wet weight) aerobes*	*anaerobes*
0–5	3,300	600
28–36	200	100
66–74	300	100
104–112	600	100
142–150	350	100
180–188	600	450
218–226	200	200

DISCUSSION

The vertical distribution of bacteria in the upper sixty centimeters of the terrigenous deposits of clays and silts examined is very similar in certain general features to that reported by previous workers. The large population at the surface, the rapid decrease in numbers of bacteria with depth, and the larger number of aerobes than anaerobes found in most cores in this investigation have also been reported by Reuszer (1933), ZoBell and Anderson (1936) and others. However, there are great enough differences in the numbers and distribution of bacteria in the various cores examined to make one question the advisability of generalizing such data. Without discussing the specific factors which account for these differences, it can be said that they are due to extreme vertical and lateral variability in the bottom materials themselves. It follows that "average" distribution curves of bacteria are of value only when they apply to a well-defined, homogeneous sediment.

The bacterial population of the sediments buried under more than 60 centimeters is of special interest since no previous observations have been reported for these deeper layers. The data show that both aerobic and anaerobic bacteria are present at a considerable distance beneath the ocean floor. Even though cores as long as 355 centimeters were examined, a lower boundary of the bacterial population was not reached. The numbers of bacteria demonstrated in these lower levels was uniformly small in those samples analyzed immediately after collection. ZoBell (1938) has shown that the number of bacteria increase two- to fourfold after storage at 0° C. for 48 hours. The larger populations found in the samples stored for sixty hours or over may therefore be due in part to multiplication of bacteria after obtaining the core. Since only the stored cores showed high populations in the lower levels one might conclude that the populations *in situ* below 60 centimeters are always small. Only a small number of cores were examined, consequently this apparent relationship may be due to entirely different, unrecognized factors. The multiplication of bacteria in the sediments during storage shows that these muds are capable of supporting many more bacteria than are usually found, and it is possible that under certain circumstances the population *in situ* in deeply buried layers may approach that of the surface layer.

The small number of anaerobes found in the lower layers is quite puzzling. The green clays and silts contain an abundance of organic matter (Revelle and Shepard, 1939) and are very reducing in nature (ZoBell, 1935), often containing free hydrogen sulphide in the subsurface layers. These characteristics should all be conducive to an

abundant anaerobic microflora. Part of the reason for the paucity of anaerobes detected may lie in the method of making the counts, since the oval-tube procedure has the same limitations as any indirect method of enumerating bacteria based on the counting of colonies developing on a single medium. Very little information is available on the type of substrate best suited for growing the maximum number of a naturally-occurring mixed microflora of anaerobes. It is quite probable that the nutrient medium used in this investigation is not suitable for the bacteria existing on the relatively resistant organic compounds occurring in sediments which have been subjected to intensive aerobic and anaerobic decomposition.

The recovery of viable bacteria from deep layers of sediment is not proof of their activity in that material. It is well known that spores exist for long periods in a quiescent state and there is a growing belief that non-spore-forming bacteria may also have some type of resting stage. The isolation of aerobic, non-sporulating bacteria from the anaerobic environment of these sediments lends some support to this belief. As pointed out by ZoBell (1938), the small number of bacteria present in the lower layers may represent dormant survivals of the active population present when the sediment was first laid down. The opposite hypothesis, that most of the bacteria demonstrated are active *in situ,* and that the small numbers present (allowing for the limitations of the enumeration procedures) result from various unfavorable environmental conditions such as low temperature, low water content, and other inimical factors, seems equally probable.

The occurrence of discontinuous zones of bacterial populations in the same loci where there are abrupt changes in the physical and chemical properties of the sediments is a striking example of the relation between population and environment. It is of interest to point out that the observation of such biological zonation can serve to focus attention on changes in physical or chemical properties which might otherwise be overlooked.

Core F 72 is the only pelagic deposit represented in this series and to the best of the author's knowledge the data presented is the only report in the literature on the vertical distribution of bacteria in such sediments. The number of viable bacteria recovered from this material is much smaller than from the terrigenous deposits. Even though only one pelagic sample has been analyzed, it is believed that small bacterial populations will be characteristic of all such deposits. This conclusion is based on the very slow rate of deposition of these sediments, estimated to be less than a centimeter every thousand years, and on the correspondingly long period of oxidation undergone before the

material is buried beneath the ocean floor (Revelle, 1940). As a consequence most of the utilizable organic matter would be decomposed while the sediment was in contact with oxygen-bearing bottom water leaving very little for bacteria to multiply upon immediately below the surface of the deposit. It is hoped that more pelagic sediments will be available in the near future so that additional data can be gathered on this point.

SUMMARY

The numbers of aerobic and anaerobic bacteria present at various depths in cores of marine sediments up to 355 centimeters in length were determined.

Viable bacteria were found in the bottom of the longest cores examined although in most instances the number present was very small.

The numbers of bacteria found vary greatly from core to core at corresponding depths and also vertically in individual cores. A decrease in bacterial population with depth was usually observed. Many more aerobes than anaerobes were demonstrated even though conditions below the surface of the sediments appeared to be more favorable for anaerobic growth. The smaller number of anaerobes found may be partly due to limitations in the enumeration procedure.

In certain sediments, zones of high bacterial population were found beneath zones of low population. In two instances the location of such zones corresponded exactly with the loci of abrupt changes in other characteristics of the sediments.

The number of bacteria demonstrated in the one pelagic deposit examined was much smaller and more constant than in the terrigenous deposits.

ACKNOWLEDGMENT

I wish to thank Dr. F. P. Shepard and Dr. R. Revelle through whose cooperation the sediment samples were made available. I also wish to acknowledge the helpful advice and assistance of Dr. Revelle and Dr. C. E. ZoBell during the course of this investigation.

REFERENCES

Certes, A.

1884. Sur la culture, à l'abri des germes atmospheriques, des eaux et des sédiments rapportés par les expéditions du Travailleur et du Talisman. Compt. rend. Acad. Sci., 98: 690–693.

Drew, G. H.

1912. Report of investigations on marine bacteria carried on at Andros Island. Yearbook Carnegie Inst. Washington, 11: 136–154.

Ekman, V. W.

1905. An apparatus for the collection of bottom-samples. Conseil Internat. pour l'Exploration d. la Mer., Pub. d. Circonstance, No. 27.

Emery, K. O.

1939. A new coring instrument and its relation to problems of sedimentation. Thesis, University of Illinois.

Emery, K. O., and Dietz, R. S.

1939. Telescoping in marine cores. Geol. Soc. Amer., Bull. (abst.), 50: 1908.

Fischer, B.

1894. Die Bakterien des Meeres nach den Untersuchungen der Plankton-Expedition. Ergebnisse der Plankton Expedition der Humboldtstiftung, 4: 1–82.

Gazert, H.

1912. Untersuchungen über Meeresbakterien und ihren Einfluss auf den Stoffwechsel im Meere. Deutsche Sudpolarexpedition 1901–03, 7: 235.

Lloyd, B.

1931. Muds of the Clyde Sea area. II. Bacterial content. Jour. Mar. Biol. Assoc., 17: 751–765.

McCoy, A. W., and Keyte, W. R.

1934. Present interpretations of the structural theory for oil and gas migration and accumulation. Problems of Petroleum Geology, 253–307. Amer. Assoc. Petrol. Geol., Tulsa, Okla.

Murray, J., and Renard, A. F.

1891. Report on deep-sea deposits based on the specimens collected during the voyage of the "H.M.S. Challenger" in the years 1872 to 1876. 525 pp.

Reuszer, H. W.

1933. Marine bacteria and their role in the cycle of life in the sea. III. Distribution of bacteria in the ocean waters and muds about Cape Cod. Biol. Bull., 65: 480–487.

Revelle, R.

1940. Marine bottom samples collected in the Pacific Ocean by the "Carnegie" on its seventh cruise. Carnegie Inst. Wash. (In Press).

Revelle, R., and Shepard, F. P.

1939. Sediments off the California coast. Recent Marine Sediments, 247–272. Amer. Assoc. Petrol. Geol., Tulsa, Okla.

Rittenberg, S. C., Anderson, D. Q., and ZoBell, C. E.

1937. Studies on the enumeration of marine anaerobic bacteria. Proc. Soc. Exper. Biol. Med., 35: 652–653.

Russell, H. L.

1892. Untersuchungen über im Golf von Neapel lebende Bakterien. Zeit. f. Hyg., 11: 165–206.

Waksman, S. A., Reuszer, H. W., Carey, C. L., Hotchkiss, M., and Renn, C. E.

1933. Studies on the biology and chemistry of the Gulf of Maine. III. Bacteriological investigations of the sea water and marine bottoms. Biol. Bull., 64: 183–205.

White, D. W.

1935. Metamorphism of organic sediments and derived oils. Bull. Amer. Assoc. Petrol. Geol., 19: 589–617.

ZoBell, C. E.

1935. Some preliminary observations on oxidation-reduction conditions in marine bottom deposits in the Gulf of Catalina. National Res. Coun. Bull., 98: 223–224.

ZoBell, C. E.

1938. Studies on the bacterial flora of marine bottom sediments. Jour. Sed. Petrol., 8: 10–18.

ZoBell, C. E., and Anderson, D. Q.

1936. Vertical distribution of bacteria in marine sediments. Bull. Amer. Assoc. Petrol. Geol., 20: 258–269.

Contribution No. 115

Contributions from the Scripps
Institution of Oceanography
New Series, No. 115

THE EFFECT OF OXYGEN TENSION ON THE RATE OF OXIDATION OF ORGANIC MATTER IN SEA WATER BY BACTERIA[1]

By

CLAUDE E. ZOBELL[2]

Woods Hole Oceanographic Institution

It is generally recognized that the oxygen consuming capacity of heterotrophic bacteria in water serves as a good criterion of the amount of respirable or oxidizable organic matter in the water. However, the fragmentary literature on the subject records contradictory observations on the effect of oxygen tension upon the rate of bacterial oxidations. For example, Pomeroy (1938) found the amount of oxygen consumed by diluted sewage containing from 0.7 to 17.5 cc. of oxygen per liter to be independent of the oxygen tension but Heukelekian (1936) noted the maximum consumption of oxygen in such sewage mixtures containing around 10.5 cc. of oxygen per liter. According to Waksman and Carey (1935a) organic matter in sea water is oxidized more and more slowly as the oxygen tension is reduced. Conversely ZoBell and Stadler (1940a) report that the rate of bacterial oxidation of organic matter in lake water is not influenced by the oxygen tension within the examined ranges of 0.21 to 25.5 cc. of oxygen per liter.

In order to standardize procedures for the determination of the respirable organic matter content of sea water as well as to estimate the amount of oxygen being consumed by bacteria *in situ* it is necessary to have information on the effect of oxygen tension on bacterial respiration. The far-reaching significance of such determinations is emphasized by Sverdrup (1938) who points out that a rational explanation of the distribution of oxygen is the oceans awaits information on the "amount of oxygen-consuming organic matter" at different depths and the effect of oxygen content of the water on oxygen consumption.

[1] Contribution No. 280 of the Woods Hole Oceanographic Institution.

[2] Fellow from the Scripps Institution of Oceanography, University of California, La Jolla, California.

It is a pleasure to acknowledge here the indebtedness of the author to Dr. H. U. Sverdrup, Dr. H. B. Bigelow, Dr. S. A. Waksman and Dr. C. E. Renn for encouragement and constructive criticisms and to Mr. N. Souder and Mr. C. M. Weiss for material assistance.

Reprint from SEARS FOUND. JOURN. MAR. RES.

EXPERIMENTAL

Sea water was collected in 5-gallon carboys from Buzzards Bay or Vineyard Sound and brought into the laboratory. It was filtered through No. 25 bolting silk and thoroughly shaken to insure uniformity in its bacterial and chemical composition. The water was warmed to 22° C. and distributed in 4 l. quantities in gallon bottles. Tank nitrogen, or oxygen as required, was bubbled through the water until the dissolved oxygen of the water was adjusted to the desired concentration. By using flow meters it became possible to admit almost exactly the required amount of nitrogen or oxygen. The water was siphoned into 140 ml. glass-stoppered bottles under an atmosphere of nitrogen and oxygen which was in equilibrium with the partial gas pressure of the water being bottled. The oxygen content of the first two bottles filled with water and the last two was determined at once, these being used as controls to show the initial dissolved oxygen content of the water. The remaining bottles of water were placed in a water bath at 22° C. and the oxygen content determined after different periods of incubation.

The oxygen tension of the water was determined by the Winkler technique (Thompson and Robinson, 1939) using a microburette and N/100 sodium thiosulphate for titrations. In most cases the initial quadruplicate determinations agreed to within 0.03 cc./l. and the series was discarded if the divergence of duplicates exceeded 0.10 cc./l.

The bottles, siphons and other glassware used in the experiments were cleaned with sulphuric-acid dichromate solution and thoroughly rinsed. These precautions were exercised because of the known tendency of organic matter and bacteria to accumulate on glass immersed in water (Stark et al., 1938).

Adjusting the oxygen tension of sea water by the procedures outlined above has a slight effect on the carbon dioxide tension and may alter other properties of the water but the following experiment demonstrated that neither the rate nor the amount of oxygen-consumption was influenced by such treatment. Part of a sample of sea water was transferred to each of several glass-stoppered bottles without treatment. The oxygen tension of the second portion of the water sample was reduced to 0.64 cc./l. by bubbling nitrogen through it. Part of this was then bottled and to the remainder oxygen was admitted until it approximated the oxygen content of the original sample. Oxygen was bubbled through another portion of the water sample until it contained 12.74 cc./l. Part of this was bottled and to the remainder nitrogen was admitted until the oxygen tension was reduced to approximately that of the original sample after which it was bottled. Duplicate

bottles of water receiving each treatment were analyzed after different periods of incubation in the water bath at 22° C. The results which are summarized in Table I show that within the limits of experimental error the same amount of oxygen is consumed by the respiring bacteria in sea water regardless of the treatment of the samples with nitrogen or oxygen.

The effect of oxygen tension on the rate of bacterial respiration in sea water was studied by adjusting the oxygen tension of different lots of a large sample of water collected from Buzzards Bay (6/23/39) at concentrations ranging from 0.41 to 18.04 cc./l. by treating with either

TABLE I

OXYGEN CONSUMED AFTER DIFFERENT PERIODS OF TIME AT 22° C. BY BACTERIA IN SEA WATER THE GAS TENSION OF WHICH HAD BEEN ALTERED BY BUBBLING EITHER NITROGEN OR OXYGEN OR BOTH GASES ALTERNATELY THROUGH THE WATER

Gaseous treatment	*Initial dissolved oxygen*	*Oxygen consumed after*			
		2 days	*5 days*	*10 days*	*20 days*
	cc./l.	cc./l.	cc./l.	cc./l.	cc./l.
None	5.46	0.24	0.39	0.87	1.26
Nitrogen	0.64	0.25	0.34	0.62	—
Nitrogen + oxygen	5.72	0.28	0.43	0.95	1.21
Oxygen	12.74	0.21	0.41	0.97	1.32
Oxygen + nitrogen	5.30	0.25	0.36	0.84	1.24

nitrogen or oxygen. Quadruplicates were analyzed for oxygen content at once and duplicates after different periods of incubation in the water bath at 22° C. Prior to the addition of the Winkler reagents 1.0 cc. of water from each bottle was withdrawn for estimating the bacterial populations. Appropriate dilutions were plated with nutrient sea water agar and the colonies were counted after 10 days incubation at room temperature. From these data the amount of oxygen consumed per bacterial cell was calculated by applying the formula of Buchanan and Fulmer (1930): $m = \frac{2.303\ S \log b/B}{t(b - B)}$, where m is the amount of oxygen consumed per cell per hour, S the total amount of oxygen consumed in time t, B the number of bacteria at the beginning of the experiment and b the number after time t. Table II records the amount of oxygen which was consumed by the bacteria after different periods of incubation in water containing different concentrations of oxygen and the amount of oxygen which was consumed per cell per hour during the first two days of the experiment. Although all of the requisite conditions do not prevail to make the application of the

formula of Buchanan and Fulmer strictly valid, it is noteworthy that for each oxygen tension the rate of respiration of the bacteria is found to be of the same order of magnitude.

The rate of oxygen consumption was virtually the same for water of all oxygen concentrations until the concentration of oxygen was reduced to less than 0.2 cc./l. The rate of oxygen consumption decreased after two days incubation at 22° C. Excluding the first two series in Table II which initially contained the least dissolved oxygen and in which the

TABLE II

Oxygen Consumed by Multiplying Bacteria in Sea Water Containing Different Concentrations of Dissolved Oxygen at 22° C. and the Amount of Oxygen Consumed Per Cell Per Hour During the First Two Days of the Experiment as Calculated from Data on the Bacterial Populations and the Oxygen Tension

Initial dissolved oxygen	*Oxygen consumed after*				*Oxygen consumed per cell per hour during first two days*
	1 day	*2 days*	*5 days*	*10 days*	
cc./l.	cc./l.	cc./l.	cc./l.	cc./l.	cc.
0.41	0.07	0.20	0.37	0.39	13.9×10^{-12}
0.77	0.06	0.24	0.55	0.72	9.2×10^{-12}
1.19	0.06	0.21	0.62	0.95	12.5×10^{-12}
2.36	0.08	0.26	0.56	0.91	16.1×10^{-12}
5.10	0.07	0.28	0.59	0.98	15.0×10^{-12}
8.26	0.09	0.25	0.61	0.92	14.3×10^{-12}
12.74	0.05	0.23	0.67	0.91	16.4×10^{-12}

total oxygen consumption was limited after two to five days by the amount of oxygen present, the bacteria consumed an average of 14.9×10^{-12} cc. of oxygen per cell per hour during the first two days of the experiment. The average rate had dropped to 9.5×10^{-12} cc. per cell per hour for five days and to 4.7×10^{-12} cc. for ten days. In fact, from the fifth to the tenth day of the experiment the bacteria were consuming an average of only 2.6×10^{-12} cc. of oxygen per cell per hour. The decreasing respiratory rate is attributed to the progressive utilization of the more readily oxidizable fractions of organic matter occurring in the sea water, although it may also be influenced by the age of the cells. It has been shown by Clifton and Logan (1939) and others that young cells in the logarithmic phase of growth use more oxygen than older cells. The tendency of the bacteria to adhere tenaciously to the glass walls of the bottle causing many respiring bacteria to escape detection by plating procedures is another complicating factor (ZoBell, 1936). For this reason the rate of respiration

after several days incubation may be considerably less than 2.6×10^{-12} cc. per cell per hour as estimated because there are probably as many or even more respiring bacteria which are tenaciously attached to the walls of the glass bottles than the number which are detected in the water by the conventional plate count procedure.

The enrichment of sea water with readily oxidizable substances accelerates the rate of oxygen consumption by bacteria. As has been shown by Waksman and Carey (1935b) the addition of utilizable organic matter to sea water causes a large increase in the bacterial population and oxygen consumption. According to Johnson (1936) the enrichment of sea water with 0.04 per cent of glucose increased the rate of respiration of marine bacteria 10 to 378 per cent. Similar results have been reported by ZoBell (1940) for both "resting" cells and multiplying cultures from lake water. In order to ascertain if the effect of oxygen tension on the rate of oxidation of organic matter is more pronounced in the presence of larger concentrations of readily utilizable organic matter, sea water was enriched with 0.05 per cent each of glucose and asparagine. The water was inoculated with mixed cultures of marine bacteria to give an initial bacterial population of approximately two million viable cells per cc. and the oxygen tension of different lots of the water was adjusted to range from 0.48 to 7.43 cc./l. The oxygen content of the water was determined from hour to hour and the amount of oxygen consumed was calculated. The results which are summarized in Table III show that the oxygen tension has

TABLE III

Effect of Oxygen Tension on the Oxygen Uptake of Bacteria in Sea Water Enriched with 0.05 Per Cent Each of Glucose and Asparagine

Initial	*Oxygen consumed after*				
dissolved oxygen	*2 hours*	*4 hours*	*6 hours*	*10 hours*	*16 hours*
cc./l.	cc./l.	cc./l.	cc./l.	cc./l.	cc./l.
0.48	0.05	0.15	0.31	0.48	0.48
1.14	0.06	0.14	0.34	0.91	1.14
1.97	0.07	0.18	0.38	1.01	1.46
4.15	0.04	0.12	0.35	0.95	1.53
7.43	0.03	0.17	0.40	1.04	1.61

no influence on the rate of respiration of bacteria in sea water enriched with organic matter until the oxygen tension is reduced to a very low level.

Waksman and Renn (1936) suggest that the effect of oxygen tension may be more pronounced when refractory substrates are being oxidized.

Therefore the experiment was repeated using aged sea water enriched with 0.05 per cent of ferric lignoprotein, a compound which is not readily oxidized by bacteria. The lignoprotein was obtained from Dr. Waksman. The "aged" sea water had been stored in the laboratory for several weeks to permit bacterial activity to oxidize the respirable organic matter. Controls run with this water revealed that it consumed only 0.26 cc. of oxygen per liter in 20 days at 22° C. The lignoprotein was slowly oxidized by the bacteria as indicated by bacterial multiplication and oxygen consumption but the rate of oxidation was found to be independent of the oxygen tension within the examined range of 0.41 to 8.93 cc. of oxygen per liter. The results of the experiment which has been repeated with similar findings are presented in Table IV.

TABLE IV

Effect of Oxygen Tension on the Oxygen Uptake of Bacteria Incubated at 22° C. in Aged Sea Water Enriched with 0.05 Per Cent of Ferric Lignoprotein

Initial	*Oxygen consumed after*				
dissolved oxygen	*1 day*	*2 days*	*3 days*	*5 days*	*10 days*
cc./l.	cc./l.	cc./l.	cc./l.	cc./l.	cc./l.
0.42	0.30	0.41	—	—	—
0.99	0.37	0.61	0.82	0.92	—
2.00	0.39	0.70	0.87	1.21	1.54
4.76	0.37	0.58	0.80	1.04	1.53
8.93	0.34	0.59	0.76	0.96	1.34

The lignoprotein was oxidized much more slowly than glucose or asparagine. A sample of isolated lignin purified by Bartlett and Norman (1938) was also found to be slowly oxidized by bacteria in sea water. From water enriched with 0.05 per cent of the lignin and which initially contained 0.78, 2.19, 5.30 and 9.04 cc. of oxygen per liter there was consumed an average of 0.54, 0.65, 0.57 and 0.61 cc. of oxygen respectively in 58 days at 22° C. ZoBell and Stadler (1940b) found that each of eleven different samples of purified or isolated lignins was slowly oxidized by bacteria in lake water and the rate of oxidation was independent of the oxygen tension until the latter was reduced to less than 0.3 cc. of oxygen per liter.

Waksman and Renn (1936) showed that the filtration of sea water removes an appreciable quantity of the oxygen consuming constituents and in so doing the effect of oxygen tension on the rate of oxygen consumption is amplified. The former observation has been confirmed by testing the oxygen consuming capacity of sea water treated in different

ways. Large samples of surface water were divided into three lots. The first was siphoned into glass-stoppered bottles without any treatment. The second lot was filtered through No. 25 bolting silk and then bottled. The third lot was filtered through a No. 4 sintered-glass filter and shaken to equilibrate it with air after which it was bottled. An unfiltered sample of surface water collected from Buzzards Bay (6/24/39) was found to consume 0.86 cc. of oxygen per liter in 20 days at 22° C. That which was filtered through bolting silk consumed 0.60 cc. of oxygen per liter while the sintered-glass filtered water consumed only 0.49 cc. of oxygen per liter. Unfiltered, silk-filtered and sintered-glass filtered water collected from Vineyard Sound (8/4/39) consumed 1.09, 0.75 and 0.53 cc. of oxygen per liter respectively in 20 days at 22° C.

Using the method suggested by Dr. C. E. Renn a large volume of sintered-glass filtered sea water was obtained by immersing 2-liter bottles fitted with No. 4 sintered-glass filters to a depth of ten or twelve fathoms where the hydrostatic pressure forced water into the bottles. This water from which much of the particulate and readily utilizable organic matter had been removed by the filters was tested for its oxygen consuming capacity in the presence of different concentration of dissolved oxygen. The oxygen tension of aliquot parts of the water was adjusted at different levels ranging from 0.49 to 9.05 cc./l. and the amount of oxygen consumed after different periods of incubation at 22° C. was determined. Corroborating previous findings it was found that the rate of oxygen consumption was appreciably slower in the sintered-glass filtered water than in unfiltered water collected from the same station and secondly, it was found that regardless of the more refractory characteristic and smaller concentration of the organic matter in the sintered-glass filtered water, the rate of oxidation

TABLE V

Effect of Oxygen Tension on the Oxygen Uptake of Bacteria in Sea Water Incubated at 22° C. Which Had Been Filtered *in situ* Through a No. 4 Sintered-Glass Filter

Initial	*Oxygen consumed after*			
dissolved oxygen	*2 days*	*5 days*	*10 days*	*20 days*
cc./l.	cc./l.	cc./l.	cc./l.	cc./l.
0.49	0.09	0.28	0.37	0.46
0.94	0.12	0.25	0.45	0.61
1.87	0.08	0.32	0.51	0.59
3.70	0.08	0.29	0.46	0.64
5.24	0.10	0.28	0.52	0.70
9.05	0.11	0.30	0.49	0.58

of the organic matter was independent of the oxygen tension over a wide range. The results are summarized in Table V.

In the foregoing experiments it was noted that the rate at which bacteria oxidize organic matter is not influenced by the oxygen tension of sea water until the latter is reduced to 0.2 to 0.3 cc. of oxygen per liter (see Tables II and V). Below this concentration of dissolved oxygen the rate of oxygen consumption decreases with decreasing oxygen tension. However, when corrections were made for the minute amounts of oxygen introduced by the Winkler reagents it was found that respiring bacteria are able to remove the last detectable trace of oxygen from sea water provided other conditions including utilizable organic matter do not become limiting factors.

DISCUSSION

The rate of oxidation of organic matter by bacteria in sea water does not seem to be influenced by the concentration of oxygen within the examined range of 0.3 to 12.74 cc./l. although it is influenced by the concentration of oxidizable organic matter. Apparently dissolved oxygen in sea water becomes a limiting factor in the bacterial oxidation of organic matter only when the concentration of oxygen is reduced to less than 0.3 cc. per liter. However, oxygen might become a limiting factor in localized microspheres rich in oxidizable matter such as, for example, the bodies of decomposing plankton organisms, if oxygen is consumed more rapidly than it can be replaced by diffusion from the surrounding water. Under these conditions a high oxygen tension in the surrounding water might be beneficial because it would increase the oxygen gradient and hence expedite the diffusion of oxygen to the oxygen-deficient microsphere.

According to Rashevsky (1933) the rate of oxygen consumption by protoplasm is independent of the oxygen tension except in so far as the latter might influence the diffusion or penetration rate of oxygen. Similarly Shoup (1929) concludes that "a constant and maximum rate of oxygen consumption occurs in small cells when the oxygen concentration becomes sufficient to entirely saturate the surface of the oxidative catalyst of the cell." He found that light production by photogenic bacteria, an oxidative reaction, was not dimmed until the oxygen was reduced to less than 0.1 cc. per liter.

Although most workers (Amberson, 1928, Harvey, 1928, Hyman, 1929, Shapiro, 1934, ZoBell and Stadler, 1940a) find that the respiratory rate of aquatic unicellular organisms is independent of oxygen tension over a wide range, there seem to be certain exceptions. Different bacteria may have different types of respiratory metabolism as

indicated by Schlayer's (1936) observation that 20 to 30 per cent of oxygen is optimum for the respiration of *Pneumococci* while the respiration of certain other bacteria he studied is unaffected by the concentration of oxygen until the latter is reduced to less than one per cent (about 0.2 cc. per liter). The difference may be related to the membrane permeability of the bacteria or it might be related to the e.m.f. or other peculiarities of the biological system. It is noteworthy that certain bacteria whose respiration is reported to be favored by a high concentration of oxygen, namely, *Pneumococci* (Schlayer, 1936), *Azotobacter* (Burk, 1930) and *Rhizobia* (Georgi and Wilson, 1933), are surrounded by capsular membranes which might tend to retard the diffusion of oxygen. Taylor (1935) has shown that there is a relationship between the respiratory rate and the e.m.f. of certain cells, and the e.m.f. in turn is influenced by the oxygen tension. Kempner (1937) reports that at low temperatures or with old cells the respiration of *Escherichia coli* is independent of the oxygen tension, but near the optimum temperature or with young cells the rate of respiration is a function of the oxygen tension.

The observations reported above as well as the work of Waksman and associates show that the concentration as well as the quality of the organic matter influences the rate at which it is oxidized. In general, the rate of bacterial respiration increases as the concentration of oxidizable organic matter increases but additional experiments must ascertain the range within which this generalization maintains. Working with lake bacteria ZoBell (1940) found that the optimum concentration of glucose for the respiration of lake bacteria was between 100 and 1000 mgm./l. and similar results were obtained with glycerol, asparagine and lactic acid. With this concentration of organic matter the rate of bacterial respiration independent of the favorable influence on bacterial multiplication was appreciably faster than in the presence of only 5 to 10 mgm. of organic matter per liter, the concentration which occurs in sea water. Considering that most of the organic content of sea water is highly refractory to bacterial oxidation, it appears that the concentration of organic matter is near the threshold of the requirements for bacteria which probably accounts for the paucity of bacteria in the ocean. There is no direct evidence that a lack of either utilizable nitrogen or phosphorus limits bacterial activity in the ocean although it has been demonstrated by Waksman and Carey (1935b) and Waksman and Renn (1936) that nitrogen limits bacterial activity when glucose is added to sea water.

Whereas the bacteria in sea water incubated at 22° C. consumed only 14.9×10^{-12} cc. of oxygen per cell per hour, they consumed

nearly four times as much or 54.1×10^{-12} cc. of oxygen per cell per hour at this temperature when the sea water was enriched with 0.05 per cent each of asparagine and glucose. Considering that the bacteria approximate spheres having a mean diameter of 1.0 μ and a density near that of sea water, it is estimated that in the sea they use about 30 cc. of oxygen per hour per gram of living cells and nearly four times as much (around 110 cc. per hour per gram) in the presence of an abundance of oxidizable organic matter. Heilbrunn (1937) has compiled data which show that various marine animals consume only from 0.002 to around 1.0 cc. of oxygen per hour per gram of fresh living material under comparable conditions. However, in spite of the relatively large oxygen consuming capacity of respiring bacteria, it would require a bacterial population of more than seven thousand per cc. to consume 1.00 cc. of oxygen from a liter of sea water in a year at 22° C., and proportionately more at lower temperatures. According to Johnson (1936) the Q_{10} of marine bacteria is 2.3 between 5° and 15° C. and 2.18 between 15° and 25° C.

If the results of this paper are applicable to conditions in the ocean, they have an important bearing on the explanation of the distribution of dissolved oxygen. It follows that where the concentration of oxygen is more than 0.3 cc./l. there exists no relation between the amount of oxygen consumed by bacteria and the amount present. Assuming that the bacterial oxidation of organic matter is the principal cause of oxygen consumption at depths well below the photosynthetic zone, say below 300 meters, no conclusions can be drawn concerning the rate of oxygen consumption from observations on the amount of oxygen present or vice versa because the two quantities are independent of each other. This is contrary to Sverdrup's (1938) suggested explanation of the oxygen minimum in the ocean. However, in fairness it should be added that Sverdrup emphasized the speculative character of his suggestion which was made to arouse interest in the problem. Moreover, at that time upon being consulted the author expressed the opinion that judging from reports in the literature, oxygen consumption by marine bacteria might be directly proportional to the oxygen tension, an opinion which is contradicted by the present findings.

Going a step further it appears that the distribution of oxygen in the ocean cannot be explained by considering only processes *in situ* but it is also necessary as Seiwell (1937) has done to consider the "history" of the water masses. In order to do so properly the factors which influence oxygen consumption must be studied further.

SUMMARY

The rate of oxidation of organic matter in sea water as indicated by oxygen consumption by bacteria is independent of the oxygen tension within the examined range of 0.31 to 12.74 cc. of oxygen per liter.

As the concentration of oxygen is reduced below 0.3 cc. per liter the respiratory rate decreases, although if oxidizable organic matter is present bacteria can remove the last detectable trace of dissolved oxygen from sea water.

During the first two days of incubation at 22° C. bacteria in sea water were found to consume an average of 14.9×10^{-12} cc. of oxygen per cell per hour; progressively less thereafter as the more readily oxidizable fractions of organic matter were utilized.

Although the enrichment of sea water with 0.05 per cent each of glucose and asparagine accelerates the rate of respiration, the rate in the enriched sea water is not influenced by the oxygen tension within the stated limits.

Filtering sea water through silk plankton netting or sintered-glass removes much of the more readily oxidizable matter from sea water but the rate of oxygen consumption by bacteria in the filtered water is independent of the oxygen tension.

Lignoprotein as well as a sample of purified lignin was found to be slowly oxidized by marine bacteria, the rate being independent of the oxygen tension.

The probable rôle of bacteria in influencing the distribution of dissolved oxygen in the sea is discussed.

REFERENCES

Amberson, W. R.

1928. The influence of oxygen tension upon the respiration of unicellular organisms. Biol. Bull., *55,* 79–91.

Bartlett, J. B. and Norman, A. G.

1938. Changes in the lignin of some plant materials as a result of decomposition. Soil Sci. Proc., 210–216.

Buchanan, R. E. and Fulmer, E. I.

1930. Physiology and Biochemistry of Bacteria. Williams and Wilkins Co., Baltimore, *3,* 154.

Burk, D.

1930. The influence of oxygen gas upon the organic catalysis of nitrogen fixation by *Azotobacter.* Jour. Phys. Chem., *34,* 1195–1209.

Clifton, C. E. and Logan, W. A.

1939. On the relation between assimilation and respiration in suspensions and in cultures of *Escherichia coli*. Jour. Bact., *37*, 523–540.

Georgi, C. E. and Wilson, P. W.

1933. The influence of the tension of oxygen on the respiration of *Rhizobia*. Arch. f. Microbiol., *4*, 543–564.

Harvey, E. N.

1928. The oxygen consumption of luminous bacteria. Jour. Gen. Physiol., *11*, 469–475.

Heilbrunn, L. V.

1937. An Outline of General Physiology. W. B. Saunders Co., Philadelphia, pp. 197–201.

Heukelekian, H.

1936. Oxygen tension and bacterial numbers. Sewage Works Jour., *8*, 415–421.

Hyman, L. H.

1929. The effect of oxygen tension on oxygen consumption in *Planaria* and some *Echinoderms*. Physiol. Zool., *2*, 505–543.

Johnson, F. H.

1936. The oxygen uptake of marine bacteria. Jour. Bact., *31*, 547–556.

Kempner, W.

1937. Effect of oxygen tension on cellular metabolism. Jour. Cell. and Comp. Physiol., *10*, 339–363.

Pomeroy, R.

1938. Influence of oxygen concentration on biochemical oxygen demand. Sewage Works Jour., *10*, 465–472.

Rashevsky, N.

1933. Note on the mathematical theory of oxygen consumption at low oxygen pressures. Protoplasma, *20*, 125–130.

Schlayer, E.

1936. The influence of oxygen tension on the respiration of *Pneumococci* (Type I.). Jour. Bact., *31*, 181–189.

Seiwell, H. R.

1937. The minimum oxygen concentration in the western basin of the North Atlantic. Papers in Physical Oceanogr. and Meteorology, Woods Hole Oceanographic Institution, *5*, 5–23.

Shapiro, H.

1934. The light intensity of luminous bacteria as a function of oxygen pressure. Jour. Cell. and Comp. Physiol., *4*, 313–327.

Shoup, C. S.

1929. The respiration of luminous bacteria and effect of oxygen tension upon oxygen consumption. Jour. Gen. Physiol., *13,* 27–45.

Stark,W. H., Stadler, Janice, and McCoy, Elizabeth.

1938. Some factors affecting the bacterial population of freshwater lakes. Jour. Bact., *36,* 653–654.

Sverdrup, H. U.

1938. On the explanation of the oxygen minima and maxima in the oceans. Jour. d. Conseil Internat., *13,* 163–172.

Taylor, A. B.

1935. Studies of the electromotive force in biological systems. Jour. Cell. and Comp. Physiol., *7,* 1–21.

Thompson, T. G. and Robinson, R.

1939. Notes on the determination of dissolved oxygen in sea water. Jour. Mar. Res., *2,* 1–8.

Waksman, S. A. and Carey, C. L.

1935a. Decomposition of organic matter in sea water by bacteria. I. Bacterial multiplication in stored sea water. Jour. Bact., *29,* 531–543.

Waksman, S. A. and Carey, C. L.

1935b. Decomposition of organic matter in sea water by bacteria. II. Influence of addition of organic substances upon bacterial activity. Jour. Bact., *29,* 545–561.

Waksman, S. A. and Renn, C. E.

1936. Decomposition of organic matter in sea water by bacteria. III. Factors influencing the rate of decomposition. Biol. Bull., *70,* 472–483.

ZoBell, C. E.

1936. Periphytic habits of some marine bacteria. Proc. Soc. Exp. Biol. and Med., *35,* 270–273.

ZoBell, C. E.

1940. Some factors which influence oxygen consumption by bacteria in lake water. Biol. Bull., *78,* 388–402.

ZoBell, C. E. and Stadler, Janice.

1940a. The effect of oxygen tension on the oxygen uptake of lake bacteria. Jour. Bact., *39,* 307–322.

ZoBell, C. E. and Stadler, Janice.

1940b. The oxidation of lignin by lake bacteria. Arch. f. Hydrobiol., In press.

LIST OF CONTRIBUTIONS

from the

SCRIPPS INSTITUTION OF OCEANOGRAPHY

New Series

Number

1. Sverdrup, H. U. On the evaporation from the oceans. *Jour. Marine Research*, v. 1, p. 3-14 1937.

2. ZoBell, C. E. Studies on the bacterial flora of marine bottom sediments. *Jour. Sed. Petrol.*, v. 8, p. 10-18, 1938.

3. Allen, W. E. Non-visible specimens. *Turtox News*, v. 16, p. 1-3, 1938.

4. Sverdrup, H. U. Notes on erosion by drifting snow and transport of solid material by sea ice. *Amer. Jour. Sci.*, v. 35, p. 370-73, 1938.

5. ZoBell, C. E., and S. C. Rittenberg. The occurrence and characteristics of chitinoclastic bacteria in the sea. *Jour. Bacter.*, v. 35, p. 275-87, 1938.

6. Natland, M. L. New species of foraminifera from the west coast of North America and from later Tertiary of the Los Angeles Basin. *SCRIPPS INSTITUTION BULLETIN*, tech. ser., v. 4, p. 137-64, 1938.

7. LaFond, E. C. Relationship between mean sea level and sand movement. *Science*, v. 88, p. 112-13, 1938.

8. Myers, E. H. The present state of our knowledge of the life history of the foraminifera. *Nat. Acad. Sci., Proc.*, v. 24, p. 10-17, 1938.

9. Sumner, F. B., and P. Doudoroff. Some experiments upon temperature acclimatization and respiratory metabolism in fishes. *Biol. Bull.*, v. 74, p. 403-29, 1938.

10. Young, R. T. The effect of balanced versus unbalanced solutions of pH and distilled water on fish. *Ecology*, v. 19, p. 126-40, 1938.

11. McEwen, G. F. Modern dynamical oceanography: an achievement of application to ocean observations of principles of mechanics and heat. *Philos. Soc., Proc.*, v. 79, p. 145-66, 1938.

12. Allen, W. E. Quantity collecting of planktonic diatoms. *Science*, v. 87, p. 171-72, 1938.

13. Shepard, F. P., and G. E. Macdonald. Sediments of Santa Monica Bay, California. *A. A. P. G., Bull.*, v. 22, p. 201-16, 1938.

14. Cupp, E. E., and W. E. Allen. Plankton diatoms of the Gulf of California. *Allan Hancock Pacific Exped.*, v. 3. p. 61-99, 1938.

15. Sverdrup, H. U. On the process of upwelling. *Jour. Marine Research*, v. 1, p. 155-64, 1938.

16. ZoBell, C. E., and H. D. Michener. A paradox in the adaptation of marine bacteria to hypotonic solutions. *Science*, v. 87, p. 328-29, 1938.

17. Fox, D. L., and C. R. Moe. An Astacene-like carotenoid from a Pacific Coast anemone, *Epiactis prolifera*. *Nat. Acad. Sci., Proc.*, v. 24, p. 230-35, 1938.

Number

18. Gordon, R. D. Note on estimating bacterial populations by the dilution method. *Nat. Acad. Sci., Proc.*, v. 24, p. 212-15, 1938.

19. Young, R. T. The life history of a trematode (*Levinseniella cruzi?*) from the shore birds (*Limosa fedoa* and *Catoptrophorus semipalmatus inornatus*). *Biol. Bull.*, v. 74, p. 319-39, 1938.

20. Johnson, M. W. Concerning the copepod *Eucalanus elongatus* Dana and its varieties in the northeast Pacific. *SCRIPPS INSTITUTION BULLETIN, tech. ser.*, v. 4, p. 165-80, 1938.

21. Allen, W. E. "Red water" along the west coast of the United States in 1938. *Science*, v. 88, p. 55-56, 1938.

22. Sverdrup, H. U. On the explanation of the oxygen minima and maxima in the oceans. *Jour. du Conseil*, v. 13, p. 163-172, 1938.

23. Sverdrup, H. U. Research within physical oceanography and submarine geology at the Scripps Institution of Oceanography during April 1937 to April 1938. *Amer. Geophys. Union, Trans.*, p. 238-42, 1938.

24. Fleming, R. H. Tides and currents in the Gulf of Panama. *Jour. Marine Research*, v. 1, p. 192-206, 1938.

25. McEwen, G. F. Some energy relations between the sea surface and the atmosphere. *Jour. Marine Research*, v. 1, p. 217-38, 1938.

26. Monk, C. R. An aqueous medium for mounting small objects. *Science*, v. 88, p. 174-76, 1938.

27. Evans, R. D., A. F. Kip, E. G. Moberg. The radium and radon content of Pacific Ocean water, life and sediments. *Amer. Jour. Sci.*, v. 36, p. 241-59, 1938.

28. Ritter, W. E. Dr. Fred Baker. *Science*, v. 88, p. 48-49, 1938.

29. Coe, W. R. Influence of association on the sexual phases of gastropods having protandric consecutive sexuality. *Biol. Bull.*, v. 75, p. 274-85, 1938.

30. Marks, G. W. The copper content and copper tolerance of some species of mollusks of the southern California coast. *Biol. Bull.*, v. 75, p. 224-37, 1938.

31. Sumner, F. B., and P. Doudoroff. Some effects of light intensity and shade of background upon the melanin content of Gambusia. *Nat. Acad. Sci.*, v. 24, p. 459-63, 1938.

32. Sumner, F. B., and P. Doudoroff. The effects of light and dark backgrounds upon the incidence of a seemingly infectious disease in fishes. *Nat. Acad. Sci., Proc.*, v. 24, p. 463-66, 1938.

33. Coe, W. R. Sexual phases in the gastropod *Crucibulum spinosum*. *Jour. Morphology*, v. 63, p. 345-61, 1938.

34. Allen, W. E. The Templeton Crocker Expedition to the Gulf of California in 1935—The phytoplankton. *Amer. Microsc. Soc., Trans.*, v. 57. p. 328-35, 1938.

Number

35. ZoBell, C. E. The sequence of events in the fouling of submerged surfaces. *Official Digest, Fed'n Paint and Varnish Prod. Clubs*, no. 178, p. 379-85, 1938.

36. Coe, W. R. A new genus and species of Hoplonemertea having differential polar sexuality. *Zoologischer Anzeiger*, v. 124, p. 220-24, 1938.

37. Gordon, R. D., and C. E. ZoBell. Note on the successive dilution method for estimating bacterial population. *Zentralbl. f. Bakteriol.*, II Abt., Bd. 99, p. 318-20, 1938.

38. Fox, D. L. An illustrated note on the mating and egg-brooding habits of the two-spotted octopus. *San Diego Soc. Nat. Hist., Trans.*, v. 9, p. 31-34, 1938.

39. Shepard, F. P., and C. E. LaFond. Undertow—A discussion. *Science*, v. 89, p. 78-79, 1938.

40. ZoBell, C. E., and C. B. Feltham. Bacteria as food for certain marine invertebrates. *Jour. Marine Research*, v. 1, p. 312-27, 1938.

41. ZoBell, C. E. and J. H. Long. Studies on the isolation of bacteria-free cultures of marine phytoplankton. *Jour. Marine Research*, v. 1, p. 328-34, 1938.

42. Doudoroff, Peter. Reactions of marine fishes to temperature gradients. *Biol. Bull.*, v. 75, p. 494-509, 1938.

42-A. Fox, D. L., and M. C. Sargent. Variations in chlorophyll and carotenoid pigments of the brine flagellate, *Dunaliella salina*, induced by environmental concentrations of sodium chloride. *Chem. and Industry*, v. 57, p. 1111, 1938.

43. Allen, W. E. Surface distribution of marine plankton diatoms in the Panama region in 1933. *SCRIPPS INSTITUTION BULLETIN, tech, ser.*, v. 4, p. 181-96, 1939.

44. Emery, K. O. Rapid method of mechanical analysis of sands. *Jour. Sed. Petrol.*, v. 8, p. 105-111, 1938.

45. Sverdrup, H. U. Second note on the logarithmic law of wind structure near the ground. *Royal Meteor. Soc., Quart. Jour.*, v. 65, p. 57-60, 1939.

46. ZoBell, C. E. The biological approach to the preparation of anti-fouling paints. *Sci. Section, Nat'l Paint, Varnish and Lacquer Assoc., Proc.*, Circular 588, p. 149-63, 1939.

47. Sverdrup, H. U. On the influence of stability and instability on the wind profile and the eddy conductivity near the ground. *Fifth Intern. Congr. Applied Mech., Trans.*, p. 369-72, 1939.

48. Sverdrup, H. U. Oceanic circulation. *Idem*, p. 279-293, 1939.

49. Sumner, F. B. Quantitative effects of visual stimuli upon pigmentation. *Amer. Naturalist*, v. 73, p. 219-34, 1939.

50. Sumner, F. B. Human psychology and some things that fishes do. *Scientific Monthly*, v. 49, p. 245-55, 1939.

51. Allen, W. E. Growth of a marine observatory. *Intern. Rev. d. ges. Hydrob. u. Hydrog.*, Bd. 39, p. 464-71, 1939.

Number

51-a. Fox, D. L., and C. F. A. Pantin. The biochemical basis of the colors of the plumose anemone, *Metridium senile*. *Anat. Record*, v. 75, Suppl., p. 135-36, 1939.

52. Sverdrup, H. U. Physics and geophysics. *Univ. California Faculty Research Lecture*, 23 pp., 1939.

53. Shepard, F. P., R. Revelle, R. S. Dietz. Ocean-bottom currents off the California coast. *Science*, v. 89, p. 488-89, 1939.

54. Gordon, R. D. Some preliminary postulates on stimulus-perception, and consequent probability distribution for behavior. *Psychometrika*, v. 4, p. 89-98, 1939.

55. Coe, W. R. Sexual phases in terrestrial Nemerteans. *Biol. Bull.*, v. 76, p. 416-27, 1939.

56. Allen, W. E. Microcopepoda in marine phytoplankton catches. *Science*, v. 89, p. 532-33, 1939.

57. LaFond, E. C. Variations of sea level on the Pacific Coast of the United States. *Jour. Marine Research*, v. 2. p. 17-29, 1939.

58. Allen, W. E. Cut-throat competition in the sea. *Scientific Monthly*, p. 111-19, 1939.

59. Fleming, R. H. Tables for Sigma-T. *Jour. Marine Research*, v. 2, p. 9-11, 1939.

60. Gordon, R. D. (with foreword by C. E. ZoBell). Estimating bacterial populations by the dilution method. *Biometrika*, p. 167-80, 1939.

61. Young, R. T., Jr., and R. D. Gordon. Report on the penetration of light in the Pacific Ocean off the coast of southern California. *SCRIPPS INSTITUTION BULLETIN, tech. ser.*, v. 4, p. 197-218, 1939.

62. Scheer, B. T. The development of the concept of tissue respiration. *Annals of Science*, v. 4, p. 295-305, 1939.

63. Sverdrup, H. U. Research within physical oceanography and submarine geology at the Scripps Institution of Oceanography during April 1938 to April 1939. *Amer. Geophys. Union, Trans.*, p. 422-27, 1939.

64. Johnson, M. W. *Pseudodiaptomus (Pseudodiaptallous) euryhalinus*. A new subgenus and species of Copepoda, with preliminary notes on its ecology. *Amer. Micros. Soc., Trans.*, v. 58, p. 349-55, 1939.

65. Fleming, R. H. The control of diatom populations by grazing. *Cons. Perm. Intern., Jour. du Conseil*, v. 14, p. 210-27, 1939.

66.-a. Vaughan, T. W. Presentation of the Agassiz Medal to Harald Ulrik Sverdrup. *Science*, v. 90, p. 24-26, 1939. b. Sverdrup, H. U. Response of the Medallist, *Idem*, p. 26-27, 1939.

67. ZoBell, C. E. Primary film formation by bacteria and fouling. *Collecting Net*, v. 14, 2 pp., 1939.

68. Young, R. T., Jr. Measurements on the transparency of sea-water off the coast of southern California. *Jour. Marine Research*, v. 2, p. 117-125, 1939.

Number

69. Sverdrup, H. U., and W. E. Allen. Distribution of diatoms in relation to the character of water masses and currents off southern California. *Jour. Marine Research*, v. 2, p. 131-44, 1939.

70. Fleming, R. H., and Roger Revelle. Physical processes in the ocean. In: *Recent Marine Sediments, A symposium*, p. 48-141, A.A.P.G., Tulsa, Oklahoma, 1939.

71. Revelle, Roger, and F. P. Shepard. Sediments off the California coast. *Idem*, p. 245-82, 1939.

72. ZoBell, C. E. Occurrence and activity of bacteria in marine sediments. *Idem*, p. 416-27, 1939.

73. Scheer, B. T. "Homing instinct" in salmon. *Quart. Rev. Biol.*, v. 14, p. 408-30, 1939.

74. Allen, W. E. "Phosphorescence" in the sea. *Nautical Gazette*, 2 pp., Aug. 26, 1939.

75. Sverdrup, H. U. Lateral mixing in the deep water of the South Atlantic Ocean. *Jour. Marine Research*, v. 2, p. 195-207, 1939.

76. Jacobs, W. C. A discussion of physical factors governing the distribution of microorganisms in the atmosphere. *Idem*, v. 2, p. 218-24, 1939.

77. Rittenberg, Sydney. Investigations on the microbiology of marine air. *Idem*, v. 2, p. 208-17, 1939.

78. Jacobs, W. C. Sea-level departures on the California coast as related to the dynamics of the atmosphere over the North Pacific Ocean. *Idem*, v. 2, p. 181-94, 1939.

79. Johnson, M. W. The correlation of water movements and dispersal of pelagic larval stages of certain littoral animals, especially the sand crab, *Emerita*. *Idem*, v. 2, p. 236-45, 1939.

80. Coe, W. R. Notes on the morphology and sexuality of the terrestrial Nemertean *Geonemertes palaensis*. *Bishop Museum, Occas. Papers*, p. 205-11, 1940.

81. Sumner, F. B., and M. C. Sargent. Some observations on the physiology of warm spring fishes. *Ecology*, v. 21, p. 45-54, 1940.

82. Sumner, Francis B. Further experiments on the relations between optic stimuli and the increase or decrease of pigment in fishes. *Jour. Exper. Zool.*, v. 83, p. 327-43, 1940.

83. Shepard, Francis P., and Eugene C. LaFond. Sand movements along the Scripps Institution pier. *Amer. Jour. Science*, v. 238, p. 272-85, 1940.

84. Sverdrup, H. U. The currents of the Pacific Ocean and their bearing on the climates of the coasts. *Science*, v. 91, p. 273-82, 1940.

85. Coe, W. R. Revision of the Nemertean fauna of the Pacific coasts of North, Central, and northern South America. *Allan Hancock Pacific Exped.*, v. 2, p. 247-323, 1940. (*Not available for exchange*)

86. Allen, W. E. Life in a drop of sea water. *Turtox News*, v. 18, no. 4, 3 pp., 1940.

Number

87. Emerson, Ralph, and Denis L. Fox. Gamma-carotene in the sexual phase of the aquatic fungus *Allomyces*. *Roy. Soc. London, Proc., Ser. B, No. 852*, v. 128, p. 275-293, 1940. (*Not available for exchange.*)

88. ZoBell, Claude E., and Janice Stadler. The effect of oxygen tension on the oxygen uptake of lake bacteria. *Jour. Bacteriology*, v. 39, p. 307-22, 1940.

89. ZoBell, Claude E., and Janice Stadler. The oxidation of lignin by lake bacteria. *Archiv. f. Hydrobiol.*, Bd. 37, p. 163-71, 1940. (*Not available for exchange*).

90. Sverdrup, H. U. On the annual and diurnal variation of the evaporation from the oceans. *Jour. Marine Research*, v. 3, p. 93-104, 1940.

91. Sverdrup, H. U. Hydrology, Section 2, Discussion. *B.A.N.Z. Antarctic Research Expedition 1921-31, Repts., Ser. A*, v. 3, *Oceanography*, part 2, *Hydrology*, Sect. 2, p. 88-126, 1940. (*Not available for exchange.*)

92. ZoBell, Claude E., and Jean Conn. Studies on the thermal sensitivity of marine bacteria. *Jour. Bacteriology*, v. 40, p. 223-38, 1940.

93. Lyman, John, and Richard H. Fleming. Composition of sea water. *Jour. Marine Research*, v. 3, p. 134-46, 1940.

94. Sverdrup, H. U. Research within physical oceanography and submarine geology at the Scripps Institution of Oceanography during April 1939 to April 1940. *Amer. Geophys. Un., Trans.*, 1940, p. 343-46, 1940.

95. Sverdrup, H. U. Trail blazing in the Pacific. (Research in oceanography). *California Monthly*, p. 10, 11, 28, Dec., 1940. Berkeley.

96. ZoBell, Claude E. Some factors which influence oxygen consumption by bacteria in lake water. *Biol. Bull.*, v. 78, p. 388-402, 1940.

97. Sumner, Francis B. The naturalist as a social phenomenon. *Amer. Naturalist*, v. 74, p. 398-408, 1940.

98. Sumner, Francis B. Quantitative changes in pigmentation, resulting from visual stimuli in fishes and amphibia. *Biol. Reviews*, v. 15, p. 351-75, 1940.

99. Allen, W. E. Discolored sea water. *U. S. Hydrographic Bull.*, no. 2262, 3 pp., 1940.

100. Allen, W. E. "Indicator" values of phytoplankton at the Scripps Institution. *Sixth Pac. Sci. Cong., California, 1939, Proc.*, v. 3, (in press).

101. Allen, W. E. Methods of collecting phytoplankton, of microscopic study, of assembling and filing data, and of preparation for reports at the Scripps Institution of Oceanography. *Sixth Pac. Sci. Congr., California, 1939, Proc.*, v. 3, (in press).

102. Allen, W. E. Summary outline of results of more than twenty years of research on marine phytoplankton at the Scripps Institution of Oceanography. *Sixth Pac. Sci. Congr., California, 1939, Proc.*, v. 3, (in press).

103. Fleming, Richard H. Character of the currents off southern California. *Sixth Pac. Sci. Congr., California, 1939, Proc.*, v. 3, (in press).

Number

104. Fleming, Richard H. Composition of plankton and units for reporting populations and production. *Sixth Pac. Sci. Congr., Calif., 1939, Proc.*, v. 3, (in press).

105. Fleming, Richard H. A contribution to the oceanography of the Central American region. *Sixth Pac. Sci. Congr., California, 1939, Proc.*, v. 3, (in press).

106. Johnson, Martin W. The study of species formation in certain Eucalanus copepods in the North Pacific. *Sixth Pac. Sci. Congr., California, 1939, Proc.*, v. 3, (in press).

107. La Fond, Eugene C. Sand movements near the beach in relation to tides and waves. *Sixth Pac. Sci. Congr., California, 1939, Proc.*, v. 2, p. 795-99, 1940.

108. Sargent, Marston C. A theoretical definition of productivity. *Sixth Pac. Sci. Congr., California, 1939, Proc.*, v. 3, (in press).

109. Sverdrup, H. U. The Gulf of California. Preliminary discussion of the cruise of the *E. W. Scripps* in February and March, 1939. *Sixth Pac. Sci. Congr., California, 1939, Proc.*, v. 3, (in press).

110. Sverdrup, H. U. The Scripps Institution of Oceanography from 1933 to 1938. *Sixth Pac. Sci. Congr., California, 1939, Proc.*, v. 3, (in press).

111. Shepard, Francis P. Submarine geology and geophysics. *Nature*, v. 146, p. 431-32, 1940.

112. Scheer, Bradley T. Some features of the metabolism of the carotenoid pigments in the California sea mussel (*Mytilus californianus*). *Jour. Biol. Chem.*, v. 136, p. 275-99, 1940.

113. Sverdrup, H. U. The unity of the sciences of the sea. *Sigma Xi Quart.*, v. 28, p. 105-15, 1940.

114. Rittenberg, Sydney C. Bacteriological analysis of some long cores of marine sediments. *Jour. Marine Research*, v. 3, p. 191-201, 1940.

115. ZoBell, Claude E. Effect of oxygen tension on the rate of oxidation of organic matter in sea water by bacteria. *Jour. Marine Research*, v. 3, p. 211-23, 1940.